Associations between estuarine foundation species and their effect on biodiversity across latitudes and seasons

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Derek Albert Gerber

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Senior Supervisor:
Dr. Mads S. Thomsen
Co-Supervisor:
Dr. Sarah P. Flanagan

Abstract

Seagrass, seaweed, and bivalves are ubiquitous foundation species in estuarine ecosystems that often have positive impacts on biodiversity. However, relatively little is known about their distribution patterns on the South Island of New Zealand (specifically, *Zostera muelleri*, *Ulva* spp. and shell deposits from the ubiquitous cockle *Austrovenus stutchburyi*) and their effects on local biodiversity across spatiotemporal scales. To address this research gap, nine estuaries were sampled in winter 2020 across tidal elevations and along a latitudinal gradient from 41°S to 46 °S, and in two estuaries around the Banks Peninsula (every month from November 2020 to October 2021). Small- and large-scale sampling methods were used to quantify co-occurrence patterns between foundation species (Chapter 2) and their effects on associated plant and animal communities (Chapter 3) in both the latitudinal and seasonal surveys. Such multifactorial baseline data collected across spatiotemporal scales are important to gauge how estuaries may be affected by future stressors, like eutrophication, warming, and other anthropogenic stressors.

In Chapter two, geotagged small scale digital photos and large-scale drone images were collected and analysed for percent cover of foundation species across latitudes and seasons. I found strong effects of latitude and season on the abundance of all foundation species, and results were consistent between scales. *Zostera* was most abundant in southern estuaries and in winter months whereas surface deposited shells were most abundant in northern estuaries and also in winter months. By comparison, *Ulva* was generally found in low abundances but was relatively common in the Avon Heathcote Estuary in summer months. I also found negative correlations between seaweed and seagrass suggesting that *Ulva* may have negative effects on *Zostera*, for example through competition for light or by creating adverse environmental conditions such as low oxygen levels.

In Chapter three, species-habitat-associations were quantified in quadrats (e.g., limpets attached to shells, crabs hiding under seaweed) and invertebrate abundances and taxonomic identities were quantified from cores collected in bare mud, seagrass beds and seaweed mats. Quadrats and cores were collected from the same latitudes and seasons as described in Chapter 2, but also included sampling across two elevation levels. The quadrate data showed that abundances and richness of habitat-interactions were highest in the central estuaries at low elevation and in summer months. This survey highlighted that dead bivalve shells, a habitat often ignored in estuarine surveys, were common across estuaries, seasons, and elevations (as also shown in Chapter 2) and that shells had positive effects on biodiversity.

Examples of habitat-interactions that explained much of the multivariate variability in community structures included *Ulva*-on-shell, *Notoacmea*-on-*Diloma, Diloma*-on-shells, *Notoacmea*-on-shells, and *Micrelenchus*-on-shells, again highlighting the importance of shells providing habitat for estuarine epifauna. The sediment core data showed the same overall pattern as the quadrate data, but also highlighted that estuarine foundation species are inhabited by more individuals and taxa compared to bare sediments and that abundances and richness was slightly higher in cores were seagrass and seaweed co-occurred compared to cores where foundation species were found alone. Taxa that explained most of the variation in community structure in the sediment cores included many molluscs (e.g., *Diloma, Micrelenchus, Notoacmea, Austrovenus, Zeacumantus*) again emphasising the importance of shell-forming molluscs in estuarine habitats.

The results were discussed in a context of latitudinal differences in temperature (for *Zostera*) and seasonal changes in temperature, light, desiccation, and grazing (for *Zostera* and *Ulva*) and possible differences in hydrodynamic conditions and sedimentation and erosion rates (for shells). Richness and abundances of animals were, compared to previous work done in the same regions in 2016, slightly lower, perhaps because these estuaries experienced unusually hot summers in 2017/18 and 2018/19, or they may experience stronger anthropogenic stress e.g., from eutrophication. For example, after a short marine heatwave in February 2020, I recorded a decrease in seagrass cover and less habitat-interactions, suggesting that effect from high temperature may be rapid but also short-lived. This study added multifactorial baseline data about foundation species and their associated ecological communities, from moderately-to-poorly sampled estuaries on the South Island of New Zealand. I conclude that (i) estuarine foundation species, like seagrass, seaweeds, and shells, facilitate biodiversity across spatiotemporal gradients, (ii) facilitation is slightly stronger when foundation species (here seagrass and seaweed) cooccur, and (iii) surface deposited shells are common in estuaries, also increases diversity, and therefore should be included in future surveys and experimental estuarine studies.

Acknowledgments

"The deeper you go, the weirder life gets."

-The Life Aquatic with Steve Zissou (2004)

Oh boy, this thing is finally complete! When first signing up for an adventure of this scale, I had no real idea of the highs and lows it could bring. Who would have thought in 2019 signing up for an ambitious field-based master's project would have resulted in surviving and thriving during a global pandemic, moving lab spaces, moving offices…twice, teaching myself R, and moving into a new house could all be so much fun? It sure has been one heck of an adventure!

I would first like to thank my supervisor Dr. Mads S. Thomsen, who has guided me, and supported me both mentally and financially in completing this project. Through all the trials and tribulations over the past two years, your guidance and support have made me become a better ecologist. To Dr. Sarah P Flanagan for helping and supporting me throughout this project. Thank you for all your support and guidance over these past two years.

A special thanks to my friends and colleagues in the office formally known as Office 238. It was fun while it lasted! Thank you all for the support, great chat, and heaps of coffee in our time together. To Lewis, Micaela, and Averill for always being willing to lend a hand in the field, even on the worst of days, thanks for all your help. This work would have moved at a snail's pace without your help and would have not been nearly as fun!

Thank you to my partner Kat, who has been very understanding through all my late nights, early starts, and the smell of estuary that somehow still lingers in our laundry! Your support has been monumental.

And lastly, to my parents, because without you for one would not be here today, and two for always supporting me and my goals no matter how many miles/Kilometers you or myself had to travel to get me to where I am today. Thank you very much for all your support!

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Chapter 1: Introduction

1.1. Estuaries are under siege from changing climate and other human stressors

Estuaries are semi-enclosed ecosystems where rivers meet the ocean (Hume et al. 2007, Hume et al. 2016). Estuaries are therefore characterized by strong salinity gradients and strong influences by the adjacent terrestrial, freshwater, and marine ecosystems (Kennish 2002, Hume et al. 2007, Hume et al. 2016). Estuaries are typically shallow with high benthic-pelagic coupling, and they can be highly productive because of high nutrients inputs (Blaber et al. 2000, Day Jr et al. 2012). Estuaries are important for humans because they provide ecosystem services, such as fishery grounds, attenuating storm surges, acting as nursery habitats for commercial important species, capturing, and storing blue carbon, providing refugia from predators or ameliorating abiotic stressors, as well as providing a wide variety of cultural and spiritual values (Kennish 1991, Blaber et al. 2000, Bertness et al. 2001, Kennish 2002, Angelini et al. 2011, Barbier et al. 2011, Thomsen et al. 2018b). In New Zealand, there are ca. 440 estuaries that vary wide in climate, geology, landforms, and oceanographic conditions, creating a variety of different types (Hume and Herdendorf 1988, Hume et al. 2007, Hume et al. 2016, Berthelsen et al. 2020). Within these dynamic systems, biodiversity is often supported and augmented by habitat-forming foundation species (Dayton 1972, Day Jr et al. 2012, Bible and Sanford 2016). The positioning of estuaries at the river-land-sea interface, implies that these systems, over millennia, have been hotspots of human activity and today most major cities are positioned around estuaries (Kennish 2002, McLusky and Elliott 2004, Day Jr et al. 2012). Estuaries are therefore highly modified ecosystems, that have been dramatically altered by overfishing, causeways, hard structures, altered drainage patterns, urbanisation, industrial development, introduction of invasive species, pollution with oils, heavy metals and other toxins, accelerated sedimentation, and eutrophication (Kennish 2002, McLusky and Elliott 2004, Day Jr et al. 2012). Because of their shallow semi-enclosed geomorphology, estuaries can also be susceptible to diffusive anthropogenic stressors, like climate changes and heatwaves (Kennish 1991, 2002, Diaz et al. 2008, Grilo et al. 2011, Wetz and Yoskowitz 2013, Cheng et al. 2015, Robins et al. 2016). Understanding how estuarine ecosystems and their biological communities adapt and respond to anthropogenic stress is imperative to manage and conserve these important systems.

1.2. Estuarine foundation species

Foundation species provide habitat, food and refugia, ameliorate stress and provide substrate for recruitment (Dayton 1972, Ellison et al. 2005). Foundation species also control biological interactions and reduce abiotic stress (Paine and Vadas 1969, Dodson 1970, Dayton 1972, Mills et al. 1993, Power et al. 1996, Ricciardi et al. 1997, Diaz and Rützler 2001, Ellison et al. 2005, Altieri and Witman 2006, Angelini et al. 2011, Schmidt et al. 2011, Foster 2019). Typical foundation species in marine ecosystems include coral reefs, kelp forest, seagrass beds, mangroves, saltmarshes, and reefs build by shell-forming species, where all these – minus corals and kelp – are important in estuaries (Dayton 1972, Stachowicz 2001, Gutiérrez et al. 2003, Ellison et al. 2005, Angelini et al. 2011, Barbier et al. 2011, Osland et al. 2013). Sedimentary estuaries are relatively homogenous across a landscape, but marine foundation species create complex three-dimensional structures that transforms the landscape into a more heterogeneous diverse system (Thomsen et al. 2016, Ramus et al. 2017, Foster 2019). In New Zealand estuaries, the typical foundation species are perennial clonal seagrasses (*Zostera muelleri*), seaweeds (*Ulva* spp. and *Agarophyton chilensis* (former *Gracilaria chilensis*)), filter feeding infaunal bivalves (in particular *Austrovenus stutchburyi*) and mobile shell-forming fauna (like trochid snails) (Savage et al. 2012, Thrush et al. 2014, Gongol and Savage 2016, Thomsen et al. 2016, Foster 2019)(see also Section 1.5). Estuarine foundation species also provide essential ecosystem services like erosion control, wave and storm attenuation, filtration of organic matter, and sediment stabilization (Turner and Schwarz 2006, Turner et al. 2007, Angelini et al. 2011, Savage et al. 2012, Fraser et al. 2014, Thrush et al. 2014, Cheng et al. 2015, Gongol and Savage 2016). Estuaries in New Zealand are, like estuaries worldwide, susceptible to and affected by anthropogenic stressors and climate change (Robertson et al. 2002, van Houte-Howes et al. 2004, Bloomfield and Gillanders 2005, Nelson et al. 2015, Gongol and Savage 2016, Berthelsen et al. 2018). Human impacts are not only affecting the foundation species themselves, but also the animal communities that depend on them (Norkko 1998, Santelices and Marquet 1998, Allison 2004, Boström et al. 2006, Tomas et al. 2015). Cumulative effects often occur, e.g. small increases in temperature combined with excess nutrients can cause much stronger algal blooms (Norkko 1998, Santelices and Marquet 1998, Allison 2004, Vaquer-Sunyer and Duarte 2011, Nelson et al. 2015), and create hypoxic conditions stressing fauna and flora living underneath the algal mats (Altieri and Witman 2006, Marsden and Bressington 2009, Vaquer-Sunyer and Duarte 2011). Such elevated temperature and nutrients can have major impact on biogeochemical process of seagrasses (Borum et al. 2005, Koch et al. 2007, Lee et al. 2007,

Höffle et al. 2012), affect the physiological function of estuarine invertebrates (Pörtner and Knust 2007, Rosenzweig et al. 2008), and causing large boom and bust cycles in seaweed (Nelson et al. 2015, Siciliano et al. 2019). Cumulative impacts from co-occurring human stressors on estuarine foundation species, although likely to be common, is still poorly studies across spatiotemporal scales (Kennish 1991, 2002, Harley et al. 2006).

1.3. Spatiotemporal surveys as a research tool

Research tools used to understand changes to communities include space for time substitution (Pickett 1989, Damgaard 2019), long-term studies (Strayer et al. 1986), and experiments (Dayton 1975). Long term studies were excluded here because of time constrains associated with a MSc thesis. Furthermore, field and laboratory experiments were not done partly because of Covid 19 threats (i.e., Covid-19 could, at any time, terminate an experiment), partly because laboratory facilities closed because of earthquake risks. Laboratory and field experiments also have limited ability to identify impacts from large scale stressors like climate changes and heating. For example, it is difficult to simulate extreme climatic events both in the lab and field experiments (Wernberg et al. 2012, Smale et al. 2015, Ashton et al. 2017, Pegado et al. 2020). Space for time substitution can instead be a useful approach to detect trends in community structure across regions (Pickett 1989) and are particular common along latitudinal gradients (Willig et al. 2003, Tuya et al. 2009, Wernberg et al. 2010a, Wernberg et al. 2011b, Tuya et al. 2012, Wernberg et al. 2018). For example, quantifying distribution abundances of species across latitudes (including warm and cold regions) and seasons (including warm and cold months) allows for hypotheses to be generated about what species will be most affected in a future warmer world (Strayer et al. 1986, Pickett 1989, Damgaard 2019). Also, measuring seasonal and latitudinal changes in species distribution through repeated measures on different scales gives a greater option to detect more cryptic patterns. This study here build on work by Foster (2019) and Siciliano (2018) who also quantified distribution of estuarine foundation species and their impacts on associated ecological communities (in 2015/16) in different estuaries in the South Island. More specifically, these studies focused specifically on how co-occurring habitat formers had positive impact on biodiversity across a range of spatial scales – as done in many other types of ecosystems (Altieri et al. 2007, Thomsen et al. 2010a, Angelini et al. 2011, Thomsen et al. 2018b, Gribben et al. 2019).

1.4. Objectives and reading guidelines

The main research objectives were to test if (1) estuarine foundation species varied across spatiotemporal gradients, including latitudes, anthropogenic stress, elevation, and season, and (2) if the different foundation species had different effects on associated ecological communities and (3) if associated ecological communities also varied across the same spatiotemporal gradients. Such multifactorial baseline data are important to gauge how estuaries may be affected by future stressors, like eutrophication, warming, and other anthropogenic stressors. These tests were addressed by quantifying distribution and abundances of foundation species and their associated communities using supplementary methods across the spatiotemporal scales mentioned above. More specifically, here in Chapter 1 I introduced estuarine foundation species, study locations, study organisms and general objectives. In Chapter 2 I describe surveys that, from small-scale photos and large-scale drone images, quantify abundances of foundations species across latitudes and seasons. I hypothesized that *Zostera* and *Ulva* generally have negative associations with each other because they compete for limiting resources (Thomsen et al. 2012b) and that shells are positively associated with *Zostera* and *Ulva* because lowered hydrodynamic forcing in beds of aquatic plants can facilitate shell depositions (Prager and Halley 1999). Chapter 3 describe surveys that, from sediment cores and quadrats, quantify distributions and abundances of estuarine animals across latitudes, elevations, and seasons, associated with different types of habitats including bare mudflats, seagrasses, seaweed and scattered dead shells. Finally, Chapter 4 discuss and compare results from the two data chapters.

1.5. Study System, local foundation species and main habitat-users

During the summer of 2017-2018, New Zealand experienced its hottest summer on record (Salinger et al. 2020), with conditions exacerbated by warming events which are typical of La Niña conditions (Brandolino 2018). The combined effect of warm air temperatures and high sea surface temperature saw an overall increase of 2.1°C above normal average air temperature (Brandolino 2018). The 2018-2019 summer was also warm being 1.2°C above normal average air temperature (Fedaeff 2019). Within New Zealand, there remains a knowledge gap about how coastal communities respond to hot summers (Thomsen et al. 2019a, Salinger et al. 2020). The occurrences of marine heatwaves (as observed near Christchurch, see Fig. 1.7.7) provide an important context to understand distribution patterns of estuarine organisms.

The main study objectives were addressed by sampling foundation species and their associated communities in sedimentary estuaries in the South Island of New Zealand. The distribution and abundances of foundation species and associated communities, were quantified from nine estuaries located in three latitudinal regions (Fig.1.7.3., Table 1.8.1.) – including Nelson Haven (-41.2361, 173.316, North), Cable Bay (-41.1688, 173.442032, North), Okiwi Bay (–41.2645, 173.916763, North), Avon Heathcote (-43.549, 172.746, Central), Duvauchelle Bay (-43.752, 172.927, Central), Robinsons Bay (-43.763, 172.960, Central), Papanui Inlet (-45.8389, 170.692, South), Portobello Bay (-45.8304, 170.672, South) and Waipuna Bay (-45.7875, 170.67, South). In addition, Avon Heathcote and Duvauchelle Bay were sampled more intensively to test if foundation species and their associated communities varied across seasons. These two estuaries were chosen because seagrass, seaweeds, and shells were common and because they had been sampled extensively in the past with similar methods (Marsden and Knox 2008, Marsden and Bressington 2009, Marsden and Maclaren 2010a, Thomsen et al. 2016, Siciliano 2018, Foster 2019). The Avon Heathcote Estuary is a ca 8 km^2 bar-build estuary located within the city limited of Christchurch, New Zealand (Jones et al. 2005, Marsden and Knox 2008, Gibson 2016). Duvauchelle Bay is, by comparison a smaller (ca. 0.22 km^2) mudflat located at the end of Akaroa Harbour, on the Bank's peninsula (Fig. 1.7.5).

Estuarine foundation species of particular interest were the seagrass *Zostera muelleri*, the endemic cockle *Austrovenus stutchburyi* and seaweeds, dominated by *Ulva* spp. (Jones et al. 2005, Foster 2019). New Zealand's only seagrass species *Zostera muelleri* is a perennial, colonial species found in intertidal zones throughout New Zealand's coastal waters (Turner and Schwarz 2006, Gibson 2016). *Austrovenus* is a widely distribution intertidal bivalve (Lohrer et al. 2016) that form biogenic habitat on mudflats (Mouritsen and Poulin 2003, Mouritsen 2004) and within seagrass beds (Thrush et al. 2006, Thrush et al. 2012, Thrush et al. 2014, Lohrer et al. 2016, Woodin et al. 2016). Dead shells of *Austrovenus* often accumulate on the sediment surface where they, like other bivalve shells, can provide habitat refuge, and ameliorate intertidal desiccation stress, and thereby potentially facilitate biodiversity (Posey et al. 1999, Lehnert and Allen 2002, Gutiérrez et al. 2003, Tolley and Volety 2005, Grabowski and Peterson 2007, Schejter and Bremec 2007, Gribben et al. 2009, Brett et al. 2011, Thomsen et al. 2016, Foster 2019). Still, ecological effects from surface deposited shells is poorly studied (Gutiérrez et al. 2003, Foster 2019). *Ulva* spp. is the most abundant genus of seaweed in New Zealand estuaries (Adams 1997, Jupp et al. 2007,

Marsden and Maclaren 2010b). *Ulva* is also a habitat-former and can be a primary food source for many estuarine grazers (Jorgensen et al. 2010, Johnston and Lipcius 2012, Thomsen et al. 2013, Lyons et al. 2014, Thomsen et al. 2016, Foster 2019). *Ulva* can have boom and bust cycles triggered by excess nutrient inputs sometimes causing localized hypoxia (through night-respiration and when *Ulva* decomposes) that can be detrimental to other estuarine organisms (Figueroa et al. 2009, Marsden and Bressington 2009, Marsden and Maclaren 2010b, Guidone et al. 2015, Nelson et al. 2015, Siciliano et al. 2019). Estuarine species that typically are found associated with these foundation species includes small limpets (e.g., *Notoacmea helmsii*), sea anemones (e.g., *Anthopleura aureoradiata*), various gastropods (e.g., *Diloma spp.*, *Micrelenchus tenebrosus*), and crabs (e.g., *Halicarcinus whitei*) (Jones et al. 2005, Marsden and Knox 2008, Thomsen et al. 2016, Siciliano 2018, Siciliano et al. 2019).

1.7. Figures

Figure 1.7.1. Images of foundation species

Landscape ((left) and closeup (right) images of the estuarine foundation species studied here, including *Zostera muelleri* (A-B), dead shells of *Austrovenus stutchburyi* (C-D), a live *A. stutchburyi* (E, with an attached large *Ulva*), and *Ulva* spp. (F-G).

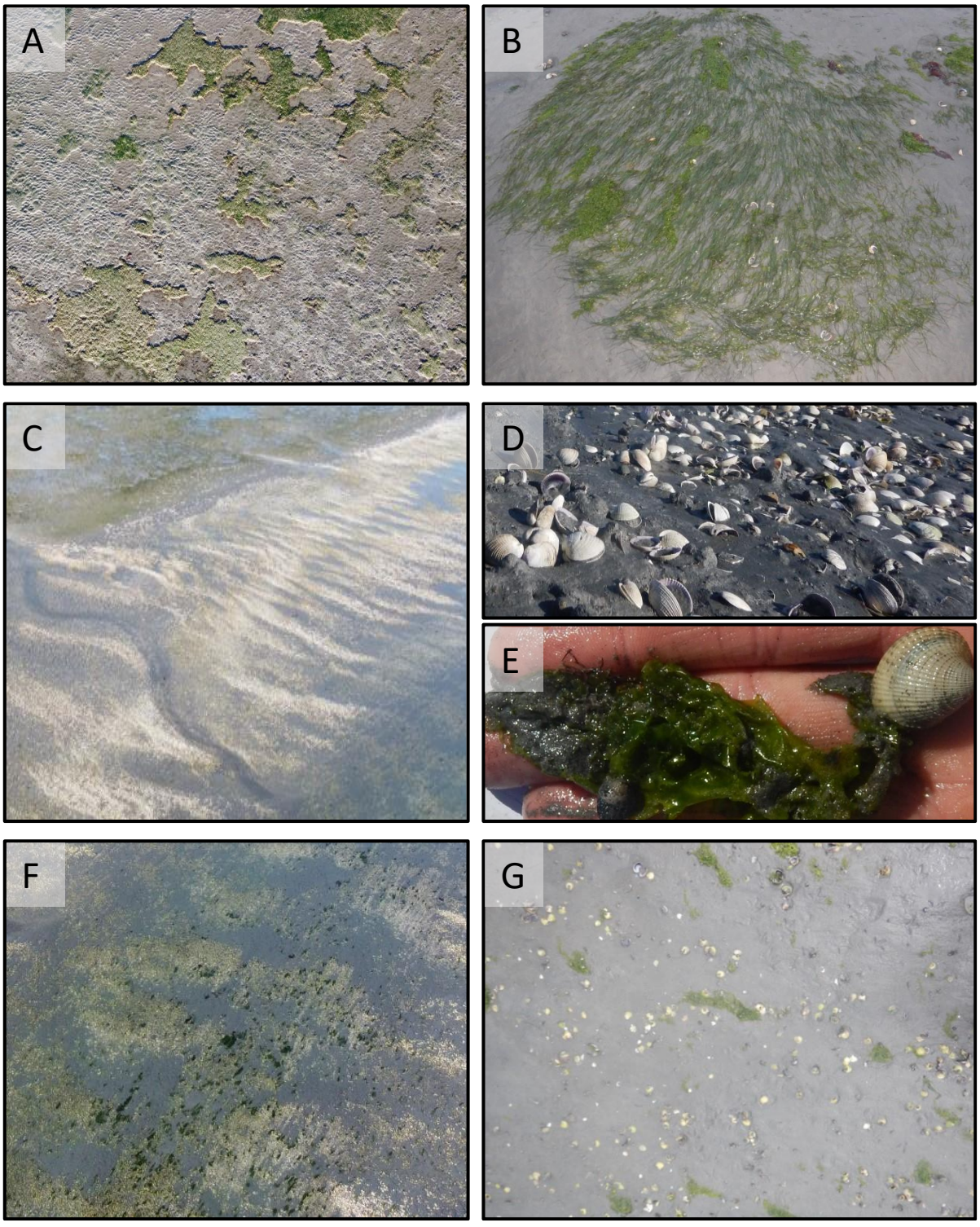


Figure 1.7.2. Methods photos

Images shows the main methods used in the thesis: a typical sample image from the large scale drone survey (A), a typical sample image from the small scale photo survey (B), a typical sample from the quadrat survey (C), example of close-up observations of three habitat-interactions in the quadrate survey (D; *Elminius modestus*, *Ulva* spp. and *Agarophyton chilensis* attached to *Austrovenus stutchburyi*), example of the content from a sediment core in a sorting tray (E), invertebrates found in the same core – including bivalves, polychaetes, crabs, gastropods and dead shells (F).

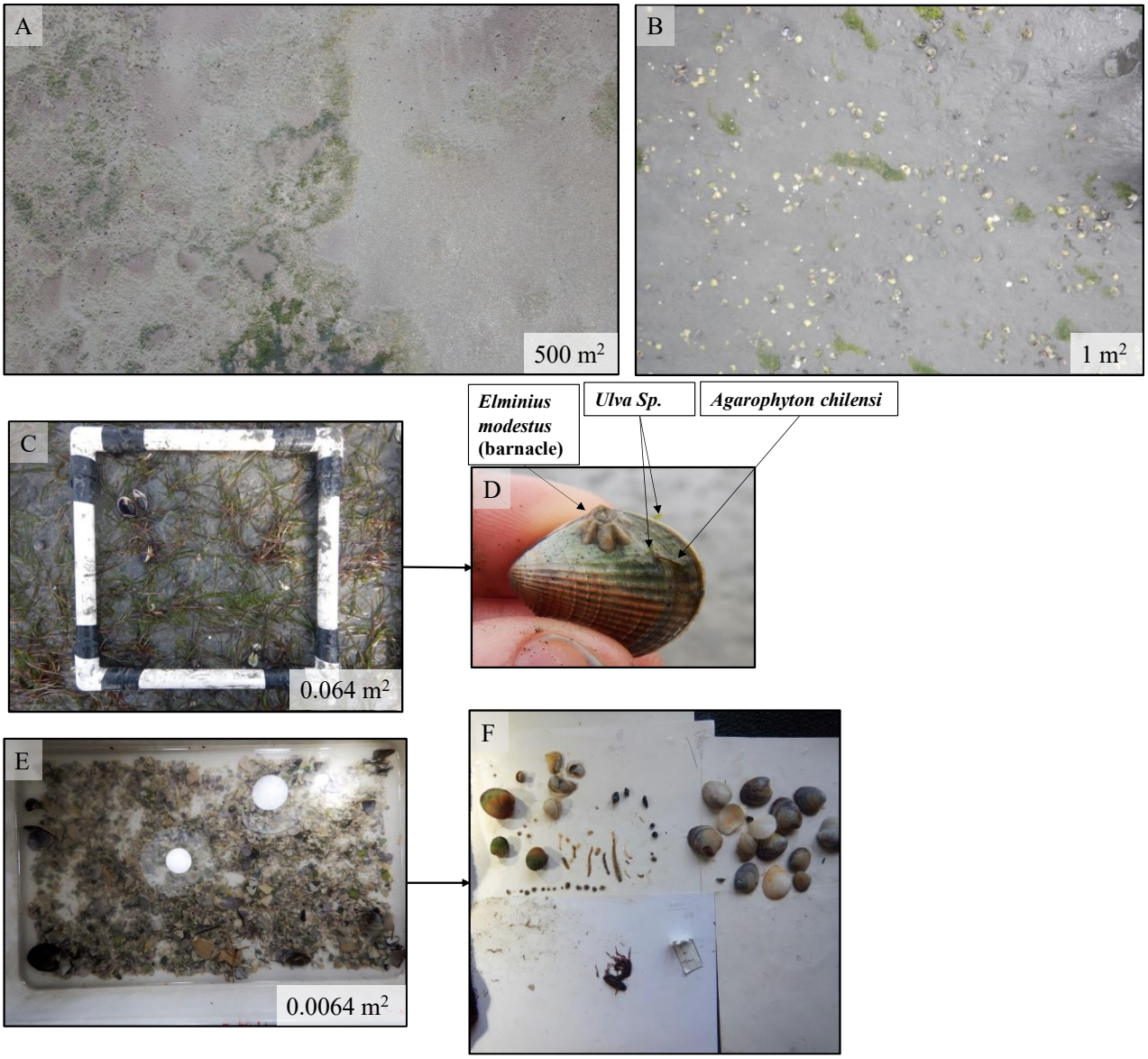


Figure 1.7.3. Study sites in the latitudinal survey

Latitudinal survey sites on the South Island of New Zealand done in winter 2020. The Avon Heathcote and Duvauchelle Bay were also sampled each month for a year. Map was created using Google Earth Pro (Google 2020).

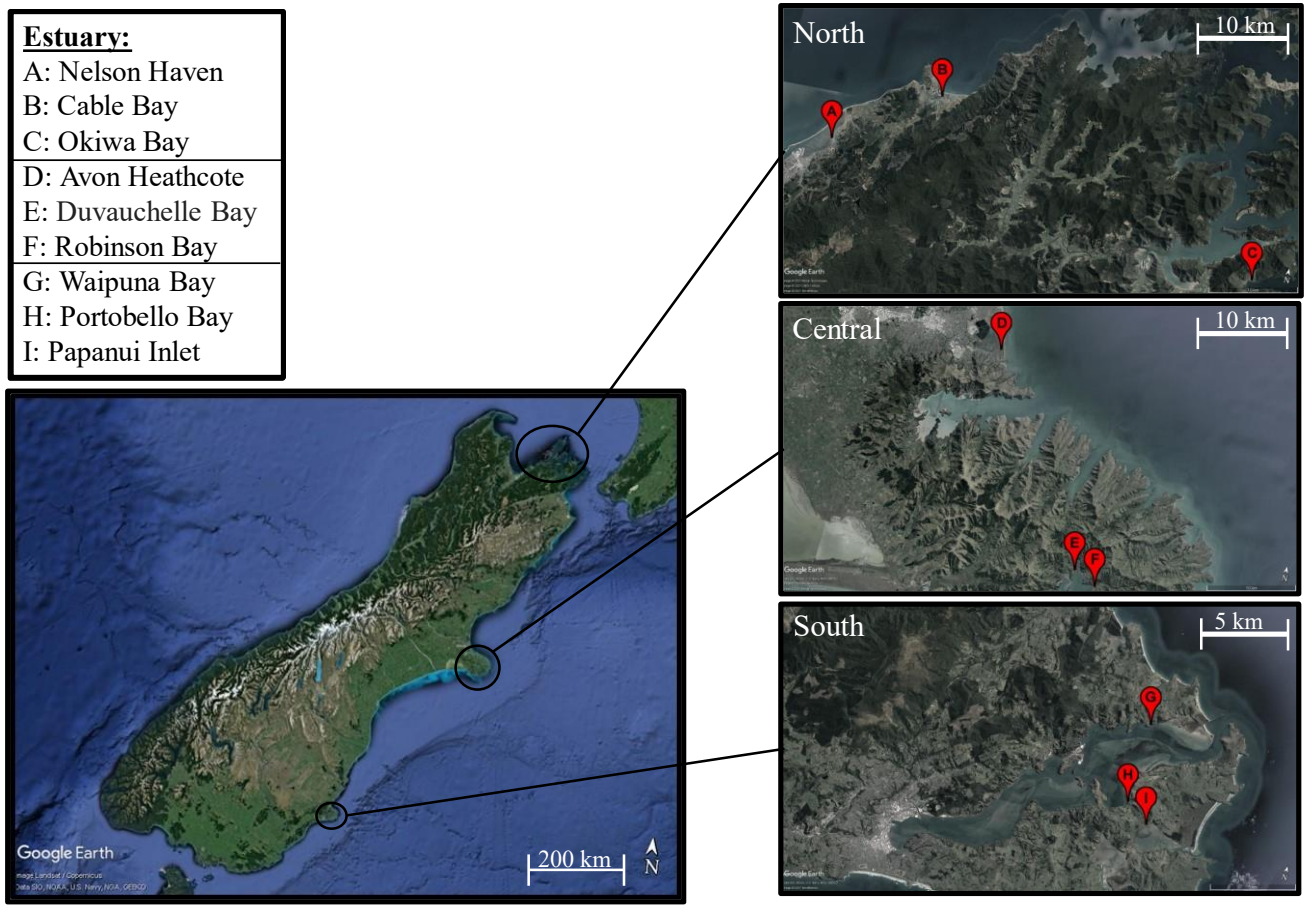


Figure 1.7.4. Study sites in the seasonal survey – quadrate sampling in the Avon Heathcote Estuary
Seasonal quadrat sampling sites located in the Avon Heathcote estuary. Map was created using Google Earth Pro (Google 2020). The top right image shows a typical landscape photo of the estuary with unvegetated mudflats and patches with seagrass and some interspersed *Ulva*.

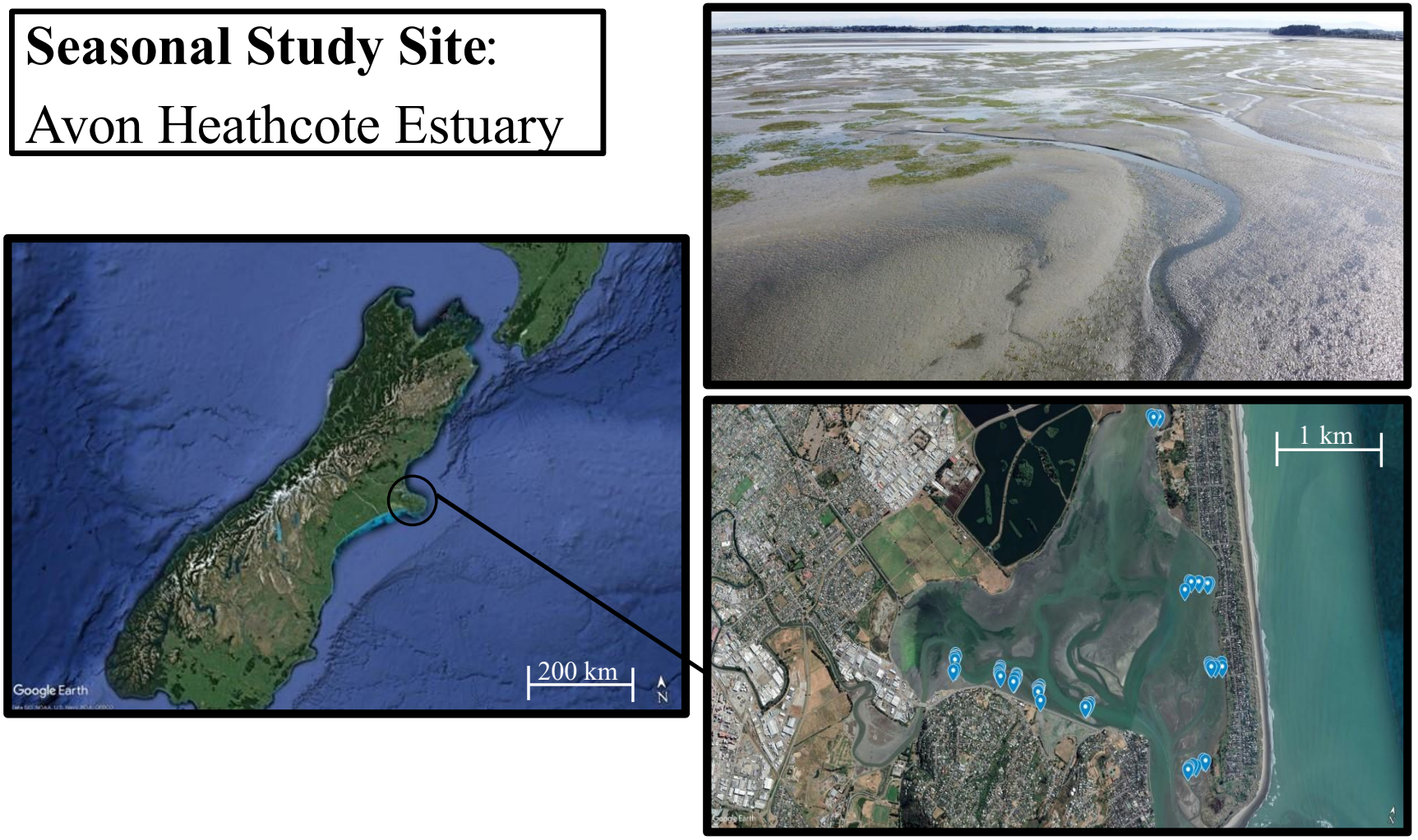


Figure 1.7.5. Study sites in the seasonal survey – quadrate sampling in the Duvauchelle Bay
Seasonal quadrat sampling sites located in Duvauchelle Bay. Maps was created using Google Earth Pro (Google 2020). The top right image shows a typical landscape photo of the estuary with unvegetated mudflats and patches with seagrass (and only little interspersed *Ulva*).

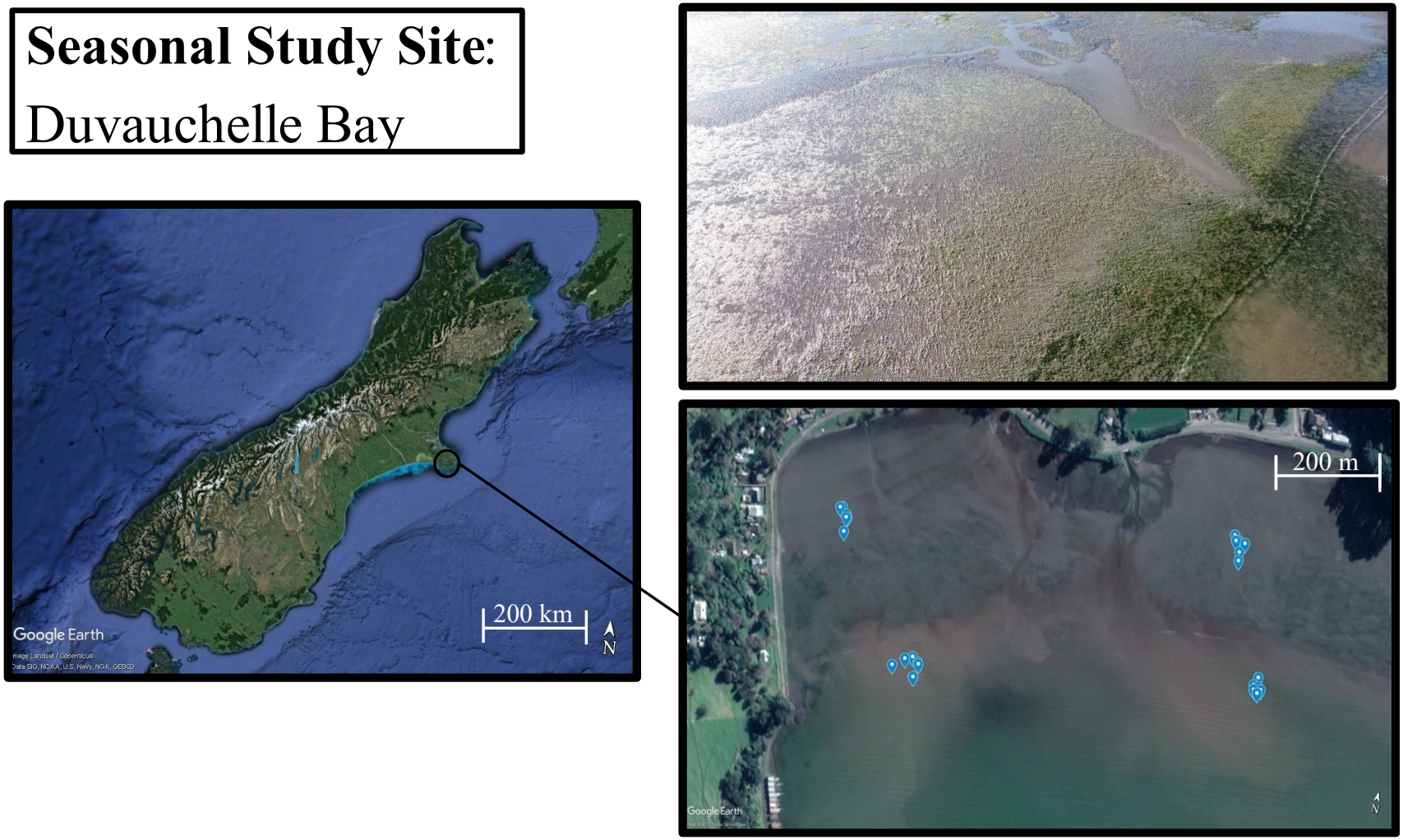


Figure 1.7.6. Study sites in the seasonal survey – drone surveys
Seasonal drone sampling sites in the Avon Heathcote Estuary including Plover Street (1) and Heron Street (2), and Duvauchelle Bay (3) on Banks Peninsula site. Map was created using Google Earth Pro (Google 2020)

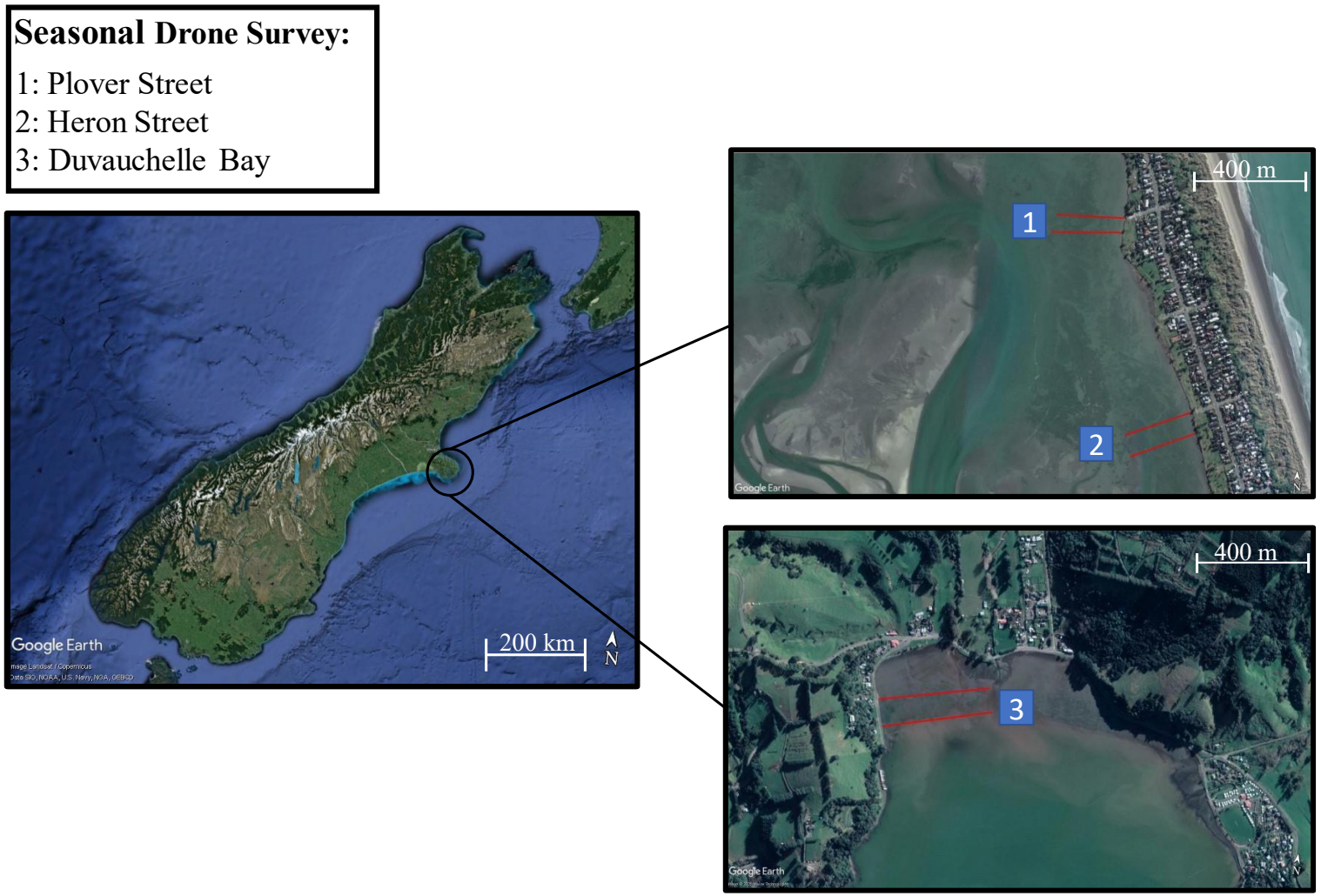
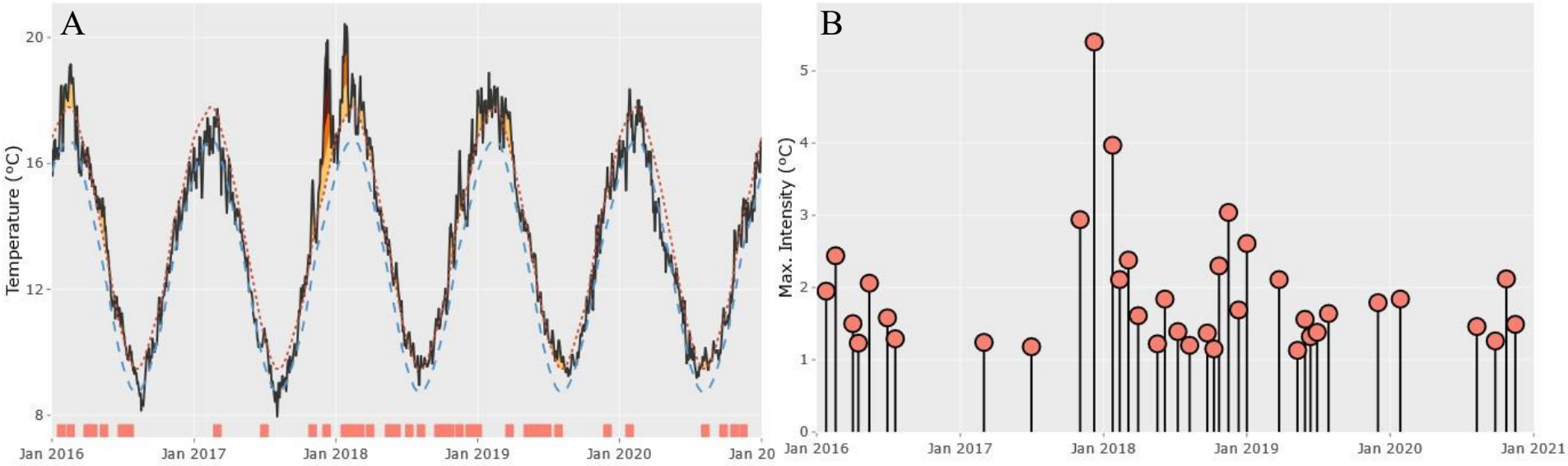


Figure 1.7.7. Sea-surface temperature and marine heatwave near Christchurch (north of Banks Peninsula), New Zealand
The figure shows absolute temperature (A), and maximum intensity (B) of marine heatwaves that occurred ca. 1 km off the coast of Christchurch, New Zealand, from December 2015 to January 2021. Maximum intensity is defined in (Hobday et al. 2016), as the highest temperature anomaly during the heatwave. Graphs were created with the Marine heatwave tracker (Schlegel 2020). Note that there were several smaller heatwaves in 2020 (B), i.e., when I did my seasonal surveys.



1.8. Tables

Table 1.8.1. Table of estuaries sampled in the latitudinal and seasonal surveys.

Table of characteristics of the sampled estuaries were estuary type were classified according to Hume et al. (2016), and anthropogenic stress is described in Chapter Two (2.2.1.) Study sites and sampling dates. The Avon Heathcote Estuary and Duvauchelle Bay were sampled in more detail in the seasonal survey.

Estuary	Latitude	Longitude	Region	Estuary type	Catchment	Anthropogenic Stress
Nelson Haven	-41.2361	173.3160	North	Tidal lagoon	Nelson Haven	High
Delaware Bay	-41.1688	173.4420	North	Tidal lagoon	Delaware Estuary	Moderate
Okiwa Bay	-41.2645	173.9168	North	Deep drowned valley	Queen Charlotte Sound	Low
Avon Heathcote	-43.5490	172.7460	Central	Tidal Lagoon	Avon-Heathcote	High
Duvauchelle Bay	-43.7520	172.9270	Central	Deep drowned valley	Akaroa Harbour	Moderate
Robinsons Bay	-43.7630	172.9600	Central	Deep drowned valley	Akaroa Harbour	Low
Papanui Inlet	-45.8389	170.6920	South	Tidal Lagoon	Papanui Inlet	High
Portobello Bay	-45.8304	170.6720	South	Deep drowned valley	Otago Harbour	Moderate
Waipuna Bay	-45.7875	170.6700	South	Deep drowned valley	Otago Harbour	Low

Chapter 2: Distribution, abundance, and associations between estuarine foundation species in the South Island of New Zealand

2.1. Introduction

Foundation species are ecologically important organisms that create habitat and refugia and control ecosystem functions (Dayton 1975, Ellison et al. 2005, Thomsen 2010). Foundation species are often sessile organisms that are abundant and modify environments (Angelini et al. 2011, Fraser et al. 2014, Cheng et al. 2015). Coastal foundation species such as kelp, fucoids, various estuarine seaweeds, oysters, corals, mangroves, and seagrasses (Angelini et al. 2011, Ramus et al. 2017, Thomsen et al. 2018b, Ellison 2019) provide ecosystem services like sediment stabilization, reduced wave attenuation, blue-carbon storage, refugia from predation, ameliorated abiotic stress, increased productivity, biodiversity, ecosystem resilience, and nursery habitats for commercial species (Angelini et al. 2011, Thomsen et al. 2018b, Ellison 2019). The most common estuarine foundation species are seagrasses, seaweeds, and surface-dwelling bivalves (Thomsen et al. 2013, Foster 2019, Fitzsimons et al. 2020, McAfee and Connell 2020, McKenzie et al. 2020). For example, clonal seagrass binds sediments and provide habitat for fish and crabs, sessile oyster and mussels create reef structures, and intertidal seaweed reduces erosion and predation effects (Coen et al. 2007, De Boer 2007, Ramus et al. 2017, Thomsen et al. 2019b). Bivalves can be foundation species, not only when they are alive, but also when dead shells accumulate on sediment surfaces (Gutiérrez et al. 2003). Dead shells can alter the biogeochemistry and physical characteristics of the sediments and provide hard substratum for the attachment of sessile organisms, and refugia from predators and abiotic stress (Kidwell and Jablonski 1983, Kidwell 2002, Casebolt and Kowalewski 2018, Foster 2019). Seagrass, seaweeds, and shells are abundant in New Zealand, although most research has focused on seagrass (Turner and Schwarz 2006, Turner 2007, Jones et al. 2008, Nelson et al. 2015, Lohrer et al. 2016, Thomsen et al. 2016, Plew et al. 2020). More specifically, estuarine foundation species in New Zealand are dominated by the seagrass, *Zostera muelleri*, different ephemeral and stress-tolerant seaweeds, like *Ulva* spp., and the endemic cockle *Austrovenus stutchburyi* (hereafter *Zostera*, *Ulva* and *Austrovenus*¸ respectively*)* (Turner and Schwarz 2006, Turner 2007, Jones et al. 2008, Ross et al. 2012, Nelson et al. 2015, Lohrer et al. 2016, Thomsen et al. 2016, Foster 2019, Plew et al. 2020). Most studies on estuarine foundation species have quantified distribution and abundances of individual species in isolation (see previous references),

although there is growing evidence that multiple foundation species often co-occur and sometimes increase biodiversity through facilitation cascades (Angelini et al. 2011, Bishop et al. 2013, Thomsen et al. 2016, Foster 2019, Gribben et al. 2019, Siciliano et al. 2019).

Estuaries in New Zealand are exposed to a variety of anthropogenic stressors, including elevated sediment and nutrient levels, heavy metals, plastics and other pollutants, altered drainage patterns, restricted flow from causeways, climate changes, and marine heatwaves (Thomsen et al. 2009, Berthelsen et al. 2018, Anon. 2019, Oliver et al. 2019, Berthelsen et al. 2020, Salinger et al. 2020). For example, many coastal foundation species have already been stressed by heatwaves (Smale et al. 2019, Straub et al. 2019) and one of the world's most extensive seagrass habitats (Shark Bay, Western Australia) declined sharply after the extremely hot summer of 2010/11 (Fraser et al. 2014, Thomson et al. 2015). Similar heatwaves have recently been observed in New Zealand (Thomsen et al. 2019a, Salinger et al. 2020), but it is unknown if estuarine foundation species were affected. To understand how estuarine foundation species will respond to increasing levels of these types of stress and to manage future populations requires baseline data about their distribution, abundance, and co-occurrence patterns. Such baseline data should be collected with standardized and rigorous methods across spatiotemporal scales (Caughlan and Oakley 2001, Nichols and Williams 2006, Berthelsen et al. 2018, Berthelsen et al. 2020). Currently, these data are lacking for many estuarine foundation species on the South Island of New Zealand.

To address this research gap, I quantified the distribution, abundance, and co-occurrence patterns of *Zostera*, *Ulva* and surface deposited shells on the South Island of New Zealand. Specifically, I asked (a) if abundances and distribution of estuarine foundation species change across season and latitude? And (b) do surface deposited shells, *Zostera,* and *Ulva* co-occur and if so - do they have positive, neutral, or negative associations? The questions were addressed by combining surveys on small (c. 1 m^2; from camera images), and large (c. 500 m^2, from drone images) scales across a latitudinal gradient (in 9 estuaries) and across seasons (in a single estuary). I hypothesized that *Zostera* and *Ulva* generally have negative associations because they compete for limited resources (Thomsen et al. 2012b) and that shell-deposits are positively associated with both *Zostera* and *Ulva* because lowered hydrodynamic forcing facilitates shell depositions (Prager and Halley 1999).

2.2. Methods

2.2.1. Study sites and sampling dates

For the latitudinal study, foundation species were quantified in three northern, three central and three southern estuaries. Each estuary within each region, represents relatively a low, moderate, or high level of 'anthropogenic stress' (estimated from nearby population sizes, riverine nutrient inputs, etc, hereafter just 'stress', see Table 1.8.1. in Chapter 1). Specifically, I sampled in Nelson Haven (-41.2361 S, 173.316 E, North, high stress), Cable Bay (-41.1688 S, 173.442032 E, North, moderate stress), Okiwa Bay (–41.2645 S, 173.916763 E, North, low stress), Avon Heathcote (-43.549 S, 172.746 E, Central, high stress), Duvauchelle Bay (-43.752 S, 172.927 E, Central, moderate stress), Robinsons Bay (-43.763 S, 172.960 E, Central, low stress), Papanui Inlet (-45.8389 S, 170.692 E, South, high stress), Portobello Bay (-45.8304 S, 170.672 E, South, moderate stress) and Waipuna Bay (-45.7875 S, 170.67 E, South, low stress). Northern estuaries were sampled from June 1 to June 5, central from September 3 to September 11, and southern estuaries from July 22 to June 26 (all in 2020). I also sampled Avon Heathcote estuary across seasons, because there are existing temporal data for this site (Foster 2019) from between November 2019 to October 2020.

2.2.2. Study 1: Close-up survey across latitudes

Small-scale distribution patterns of *Zostera, Ulva,* dead surface shells, rocks (including boulders), and mud (substrate without rocks or foundation species) were sampled with digital photos covering transects from the upper tidal shore to the shallow subtidal zone (see map on Fig. 1.7.2. in Chapter 1). Individual 'samples' were geotagged digital images taken approximately 1 meter above and perpendicular to the substrate using a Nikon Coolpix AW130 camera. Images covered ca. 1 m^2 (Thomsen et al. 2018a) and were >1 m apart. A total of 836 samples were collected across the nine estuaries (37-149 from each estuary). I used digital images to survey small-scale distribution patterns because digital images provide a permanent record that can be revisited for checking data (Foster et al. 1991, Meese and Tomich 1992), and because many samples can be collected in a few hours during low tides (i.e., I only had the opportunity to sample a single low tide per estuary – where I also had collect drone images (this Chapter), sediment cores (Chapter 3) and do visual invertebrate surveys (Chapter 3). However, the disadvantage of this method is that abundances of co-occurring subcanopy foundation species will be underestimated (as they are covered by a larger canopy-forming foundation species) (Foster et al. 1991, Meese and Tomich 1992).

2.2.3. Study 2. Landscape survey across latitudes

The large-scale distributions of *Zostera*, *Ulva*, dead shells, rocks, and mud were sampled with drone-images. Drone surveys could not be done at Nelson Haven due to no-fly-zone regulations (Services 2021, UAVNZ 2021) or Papanui Inlet and Portobello Bay because of bad weather. Drone images were captured perpendicular to the substrate at approximately 20 meters altitude using a DJI Mavic mini (47-80 images per estuary). At each estuary, I first laid out transect tapes near the upper intertidal zone. Starting at the 50-meter mark, the drone hovered at *c*. 20 m elevation to capture, record, and ground-truth the left and right bounds of the image. These measurements were used to calculate area per image using Image J software (Rueden et al. 2017). Three 150 m transects were flown from the upper intertidal zone towards the upper subtidal zones (also at 20 meters altitude) with starting points at 0, 50 and 100 m, respectively. To correct an error in altitude readings when drone altitude reading was at 0.0 meters, the distance from the bottom of the drone to the substrate was recorded to correct altitude reading post sampling event. Images were analysed for percent cover of *Zostera*, *Ulva*, dead shells, bare mud, and rocks.

2.2.4. Study 3: Close-up survey across seasons

A close-up photo survey was done to compare the distribution of *Zostera*, *Ulva*, dead shells, rocks, and mud, in summer (February 2020, 170 samples) and winter (July 2020, 88 samples) from Heron Street in the Avon Heathcote estuary (-43.549 S, 172.746 E) using methods described for study 1.

2.2.4. Study 4: Landscape survey across seasons

Drone transects were done during spring low tide at Plover Street (-43.549 S,172.746 E) and Heron Street (-43.5496 S, 172.746 E), over ten months to quantify seasonal changes of foundation species using similar methods as described for study 2. The starting position was the same for every flight to account for GPS and altitude positioning error. Each flight started from the foreshore and continued horizontally across the bay, keeping tidal elevation consistent throughout each flight and each transect. Two transects, 200 m long and separated by a minimum of 75 m, were done at each site. A total of 160 images were captured for

Plover Street (mean of 16 per transect per month) and 147 for Heron Street (mean of 15 per transect per month. Image analysis was done as described for study 1.

2.2.5. Statistical analysis

Effect of latitude and anthropogenic stress was tested with two-way ANOVAs on percent cover of *Zostera*, *Ulva*, surface shells, rocks, and mud for the small-scale photo survey but with separate 1-way ANOVAs for the large-scale drone survey (because data was missing from three estuaries so that I could not test for interaction effects). Due to these missing data, latitudinal effects from central and northern moderate and low anthropogenic stress factors sites were also tested with a two-way ANOVA. Effect of season was tested with t-tests for the small-scale survey and 1-way ANOVA for the large-scale survey. All test factors were considered fixed, and percent cover data were arcsine transformed prior to analysis to reduce variance heterogeneity. Post-hoc Tukey Tests followed significant ANOVA results ($p \leq 0.05$) to identify specific treatment effects. Finally, non-parametric Spearman rank correlation analysis was performed on abundances between all pairs of *Zostera*, *Ulva* and shells for each of the four studies. Analysis was conducted in R (Team 2020) and figures were produced using the package ggplot2 (Wickham 2016).

2.3. Results

2.3.1. Study 1: Close-up survey across latitudes

Out of 718 images, 22% showed co-occurring *Zostera*, dead shells, and *Ulva*, 8 % *Zostera* and *Ulva*, 14% *Ulva* and dead shells, 18% *Zostera* and dead shells, 18% *Zostera* alone, 1% *Ulva* alone, 14% dead shells alone and 6% no foundation species. There were strong significant effects of latitude and stress (and their interaction) on abundances of *Zostera*, *Ulva* and shells ($p < 0.001$, minus 'stress' on *Ulva*, $p = 0.052$, Table 2.7.1). Overall, shell cover was relatively low, although the significant interaction ($p < 0.001$, Table 2.7.1) highlighted a high cover (50%) in the northern moderately stressed estuary (Cable Bay) compared to the other eight estuaries (0-25%, Fig. 2.5.1A). This result was supported by post hoc tests that showed that this estuary was driving differences in shell cover across latitude ($p < 0.001$). No other patterns could be discerned for shells. Cover of *Zostera* varied from 0 to 95% across the estuaries, with slightly higher cover in southern estuaries (Fig. 2.5.1B, Table 2.7.1). A significant interaction ($p < 0.001$) reflected that latitudinal effects were strongest at moderately, compared to higher-stressed estuaries (Fig. 2.5.1B). Post hoc tests showed this

was driven by variation within the southern estuaries, that were significantly different from central and northern estuaries ($p < 0.001$). Central and northern high-stress estuaries were also different ($p < 0.001$) but with no significant difference ($p = 0.999$) between central and southern high-stress estuaries. Cover of *Ulva* was generally low, varying from 0-20% between estuaries (Fig. 2.5.1C). A significant interaction ($p < 0.001$) highlighted that although cover was generally high in the south, cover was higher in the central estuaries represented by low and high stress levels (Fig. 2.5.1C). The post hoc tests showed that moderate stress was different from both high ($p < 0.001$) and low ($p = 0.001$) stress. *Ulva* cover also varied between south and both central and northern regions ($p < 0.001$), but not between north and central regions. Cover of mud varied widely between estuaries (from 3-80%, Fig. 2.5.1.D) being relatively high and consistent in central estuaries and varying more in southern and northern estuaries depending on stress levels. Finally, I found low cover of rocks and boulders (< 15%), except in the low stress northern estuary (48%, i.e., Okiwa Bay, Fig. 2.5.1E). There was no association between *Ulva* and *Zostera* ($p = 0.62$, $r = -0.01$, Fig. 2.5.2A) but significant negative correlation between shells and *Zostera* ($p = 0.001$, $r = -0.26$, Fig. 2.5.2B) and positive correlation between shells and *Ulva* ($p < 0.001$, $r = 0.25$, Fig. 2.5.2C) – the latter effect partly explained by a strong association observed in the moderate stressed northern estuary.

2.3.2. Study 2: Landscape survey across latitudes

Out of the 350 images, 67% showed co-occurring *Zostera*, dead shell, and *Ulva*, 8% *Zostera* and *Ulva*, 12% *Ulva* and dead shell, 4% *Zostera* and dead shells, 7% *Ulva*, 1% dead shells, 1% had no co-occurring foundation species and no images found *Zostera* alone,

The single factor ANOVAs showed significant effects of latitude on shell and *Zostera* ($p < 0.001$) but not on *Ulva* (Table 2.7.2) whereas the two-way ANOVAs (here excluding the southern estuaries) found significant single factor effects of latitude and stress on shells and Zostera ($p < 0.01$ – with an additional significant Latitude × Stress interaction for shells) but not *Ulva* ($p > 0.23$, Table 2.7.3). Highest shell cover was found in Cable Bay (a northern estuary with moderate stress, 55%, Fig. 2.5.3A) driving some of the patterns detected in the ANOVAs but post hoc tests also identified differences between Okiwa Bay (north) and Robinsons Bay and Duvauchelle Bay (central estuaries, $p < 0.001$). *Zostera* cover was highest in the low-stress southern estuary (80%) and decreasing from central to northern sites (< 50%, Fig. 2.5.3B). Post hoc tests showed significant effects between northern-central and

central-southern regions ($p < 0.001$) but not between northern and southern regions ($p = 0.224$). There were not significant effects of latitude or stress on *Ulva*, emphasizing its variable abundances across all estuaries (0-15%), with the highest cover reported in the Avon Heathcote Estuary (Fig. 2.5.3C). Cover of mud was variable across latitudes and stress factors with mean cover ranging from 10-75% (Fig. 2.5.3D). By comparison, cover of large rocks and boulders was small with greatest cover found in Cable Bay (Fig. 2.5.3E) and no clear latitudinal patterns. Like in the close-up small-scale analysis, the latitudinal landscape-scale correlation analyses found a significant negative correlation between shells and *Zostera* ($p = 0.001$, $r = -0.17$, Fig. 2.5.4B) but no relationship between *Ulva* and *Zostera* cover ($p = 0.65$, $r = -0.02$, Fig. 2.5.4A). However, in contrast to the close-up latitudinal survey, I found a negative relationship between cover of shells and *Ulva* ($p = 0.009$, $r = -0.14$, Fig. 2.5.4.C).

2.3.2. Study 3: Close-up seasonal changes

Of the 258 photos, 63% showed co-occurring *Zostera*, dead shells, and *Ulva*, 2% *Zostera* and *Ulva*, 26% *Ulva* and dead shells, 4% *Zostera* and dead shells, 4% dead shells alone whereas no images showed *Zostera* alone, *Ulva* alone, or no foundation species at all. There was significantly higher cover in winter than summer for both shells (14.45 ± 3.30 vs. 6.364 ± 1.34, $t(116) = 4.44$, $p < 0.001$, Fig. 2.5.5.A) and *Zostera* (34.58 ± 6.36 vs. 16.45 ± 3.61, $t(127) = 5.05$, $p < 0.001$, Fig. 2.5.5.B). However, the pattern was opposite for *Ulva* that had significantly higher cover in summer (24.75 ± 4.85) than winter (5.55 ± 1.63, $t(218) = 5.05$, $p < 0.001$, Fig. 2.5.5C). By comparisons, mud (Fig. 2.5.5D) and rocks (Fig. 2.5.5E) did not vary much between seasons with the former having around 50% cover and the latter only 1% cover. There was (again) no relationship between *Ulva* and *Zostera* cover ($p = 0.09$, $r = -0.12$, Fig. 2.5.6A) but significant negative correlation between shells and *Zostera* ($p < 0.001$, $r = -0.28$, Fig. 2.5.6B) and shells and *Ulva* ($p = 0.003$, $r = -0.18$, Fig. 2.5.6C).

2.3.3. Study 4: Landscape survey across seasons

Out of 435 drone images, 67% showed co-occurring *Zostera*, dead shells, and *Ulva*, 8% *Zostera* and *Ulva*, 12% *Ulva* and dead shells, 4% *Zostera* and dead shell, 0% *Zostera* alone, 7% *Ulva* alone, 1% dead shells alone, and 1% no foundation species at all. ANOVA showed significant effects on *Zostera* and *Ulva* ($p < 0.001$), but not shells ($p = 0.128$, Table 2.7.4.). Still, shell cover varied slightly throughout seasons, increasing over winter months where cover varied between 0-20%, with the greatest cover at Plover Street in August (Fig. 2.5.7A,

16.43 ± 6.35). Cover of *Zostera*, the most common biogenic habitat-former, was highly variable (15%-65%), with higher cover in winter months and in July at Heron Street (65.45 ± 10.41, Fig. 2.5.7B). Post hoc tests showed differences in *Zostera* cover between February (summer) and July (winter), August (winter), and October (spring). *Ulva* was the second most common foundation species (Fig. 2.5.7C). Cover of *Ulva* varied between 0-35%, with overall lower cover in winter month and highest cover out from Heron street in February (65% ± 5.77, Fig.2.5.7C). Post hoc tests identified differences in the cover of *Ulva* February and July, August, and October. Seasonal cover of mud (i.e., with absence of foundation species) varied between 25-65% across season, with largest cover observed in September (65% ± 6.44, Fig. 2.5.7D). I found no larger rocks or boulders in the images (Fig. 2.5.7E). Finally, I found significant negative relationships between *Ulva* and *Zostera* ($p < 0.001$, $r = -0.28$, Fig. 2.5.8A), shells and *Ulva* ($p < 0.001$, $r = -0.45$, Fig. 2.5.8C) but no relationship between shells and *Zostera* ($p = 0.10$, $r = -0.08$, Fig.2.5.8B).

2.4. Discussion

Overall, *Zostera* was the most abundant foundation species and was more abundant in southern and central estuaries. Dead shells were found on sediment surfaces across all the sampled estuaries and was most abundant in Cable bay in the northern region. Seaweeds were not particularly common, except for in summer months in the Avon Heathcote estuary, where *Ulva* could form relatively large mats. I also found negative relationships between the abundances of foundation species, with the strongest being between *Ulva* and *Zostera*.

2.4.1. Effects of latitude

Zostera was least abundant in the northern estuaries, as shown in other studies (Siciliano 2018, Foster 2019), although more estuaries should be sampled to verify this pattern. Furthermore, these abundance data should be combined with physiological measurements to test if different abundances reflect differences in ecological performance (Kerr and Strother 1985, Spalding 2003, Turner and Schwarz 2006, York et al. 2013). I also found negative relationships between *Ulva* and *Zostera* and *Ulva* probably because dense mats of *Ulva* can shade and smother seagrass and even cause anoxia at the sediment-water interface as observed in many place throughout the world (Brun et al. 2003, Marsden and Bressington 2009, Marsden and Maclaren 2010a, Olyarnik and Stachowicz 2012, Thomsen et al. 2012b, Lyons et al. 2014, Young et al. 2018, Barnes 2019). Algal smothering is even enhanced under

high temperatures (Höffle et al. 2011, Holmer et al. 2011, Höffle et al. 2012) and may therefore be more severe in the Northern estuaries. The distribution of *Ulva* spp. in New Zealand estuaries is highly variable (Heesch et al. 2009, Marsden and Bressington 2009, Marsden and Maclaren 2010a, Barr et al. 2013, Gongol and Savage 2016), as I also found here, probably because unattached mats drift with the tidal currents (Hawes and Smith 1995) and its growth rates and susceptibility to grazing vary dramatically in space and time (Geertz-Hansen et al. 1993, Morgan et al. 2003, Thomsen 2004, Thomsen and McGlathery 2007). (Turner and Schwarz 2006). Still, both *Zostera muelleri* and *Ulva* spp. are relatively stress-resistant primary producers that can tolerate high levels of desiccation, salinity changes, sedimentation burial and temperature fluctuations compared to open-water seaweeds and many other seagrass species (Hemminga and Duarte 2000, Taylor et al. 2001, Tanaka and Nakaoka 2004, Turner and Schwarz 2006, Figueroa et al. 2009, Collier and Waycott 2014). The greater abundance of *Zostera* relative to seaweed could be explained by its clonal perennial growth habit combined with its high stress-tolerance, local seasonal conditions (winter sampling where low temperatures and low light levels cooler water and air temperatures, and lack of sun) that may favour seagrass over seaweeds (Turner and Schwarz 2006, Turner 2007). In contrast to seagrass, shells were most abundant in the northern estuaries and decreased along the latitudinal gradients, a pattern observed in both the small and large scales surveys. This pattern could perhaps arise because of differences in tidal currents, with lower abundances of seagrass (in northern estuaries) facilitating infaunal bivalves and therefore eventually also deposition of their shells (Trewin and Welsh 1976, Bailey et al. 1994, Beal et al. 2020).

2.4.2. Effect of season

Seasonal patterns were similar between the small scale and large surveys showing higher abundances of *Zostera* and shells in winter and highest abundance of seaweed (*Ulva*) in summer. More specifically, *Zostera* had a summer dieback with rapid extension of beds between February and July, as has been shown in other estuaries in New Zealand (Turner and Schwarz 2006). The low abundance of *Zostera* over summer may reflect stress from high water and air temperatures (see Fig 1.7.7 in Chapter 1), combined with elevated intertidal desiccation stress because most of the seagrass beds were found in the intertidal zone (Foster 1971, Kerr and Strother 1985, Ismail 2002, Inglis 2003, Foster 2019). I found slightly more shells over winter months perhaps because stronger winter storms can remove sediments and

exposed partly buried shells (Davies et al. 1989, De Haas and Eisma 1993, Olivera and Wood 1997, Ganju et al. 2017). Dead shells were found at all locations and in all months highlighting that these understudied biogenic structures may have wide and general effect on estuarine communities (see next chapter). Dead shells are, of course, different from living biogenic structures because shells cannot 'growth' through accumulated sediments, in contrast to seagrasses (Cabaço and Santos 2007, Cabaço et al. 2008, Bunsom and Prathep 2012, Duarte et al. 2013). Over time dead shells are therefore more likely to become buried (Johnson 1957, Tomašových et al. 2014). In other words, periodic erosion events and constant mortality of bivalves, are prerequisites to maintain dead shell deposits on the sediment surfaces. Importantly, *Austrovenus* was the primary shell type found on the sediment surface and shells cover had a negative relationship with cover of seaweed. This negative relationship may be because *Ulva* attached to or deposited on live cockles decreased the bivalves' filtration capacity, or because decomposition of *Ulva* caused hypoxia-related stress (Marsden and Bressington 2009, Marsden and Maclaren 2010b, Thomsen et al. 2012b). Finally, I found that *Ulva* was most abundant in summer, with little cover during most of the year. The low abundance of *Ulva* outside the warmest summer months is likely due to a combination of low light levels and low temperatures resulting in lowered growth, combined with high grazing rates from the extremely abundant trochid snail, *Micrelenchus tenebrosus* (Geertz-Hansen et al. 1993, Morgan et al. 2003, Thomsen and McGlathery 2007, Thomsen et al. 2016, Siciliano 2018, Siciliano et al. 2019) (see also next chapter).

2.4.3. Methodological issues

The different types of surveys share methodological advantages and disadvantages because they rely on digital image capture and analyses. Importantly, abundances of individual foundation species will be underestimated if they occur underneath another foundation species, possibly an attributing factor to the negative relationships found in the correlation analyses (Meese and Tomich 1992, Martin et al. 2020). However, this was not a major problem in this study because seaweeds, that can create dense mats, generally only occurred in low abundances. In the context of my objectives, the advantages were that many samples could be collected in a short period of time and that digital photography can provide a permanent digital archive of geopositioned samples that can be revisited for data-cross checking (Meese and Tomich 1992, Martin et al. 2020). Unfortunately, flight restrictions in Nelson Haven and poor weather conditions in Portobello Bay and Papanui Inlet resulted in an

unbalanced design for drone image analyses. However, the smaller scale photo surveys generally found similar results and these data were collected from all estuaries. Furthermore, the two methods used here (i.e., combining geopositioned small scale photos with large scale drone images) supplement each other, because the photos allow for species identifications (e.g., of surface deposited shell types) and collection of data in poor weather conditions and where drones are prohibited, whereas the drone images allow sampling of difficult to reach areas (like on isolated bars) and increase the spatial scale by orders of magnitude. Still, future studies should sample many more estuaries that include more latitudinal and human-stress levels (Barr et al. 2013), analysis of tidal elevations and within-estuary locations, that sample many more estuaries in different seasons. Most importantly analyses should correlate patterns of foundation species to abiotic data collected across scales from the catchment scale to specific properties of estuaries and local site conditions (Hume et al. 2007, Hume et al. 2016). Finally, I also suggest that future studies also quantify distribution of mobile shell-forming foundation species (Altieri and Witman 2014), like snails (Foster 2019), linkages and processes between live bivalves and their dead shells, as well as do manipulative experiments to establish causal linkages and better understand the patterns described here.

2.4.4. Conclusions

This study highlights that multiple foundation species often co-occur in estuaries, adding complex biogenic patchy structures to the extensive areas of more homogeneous sediment surfaces. Effects from co-occurring foundation species on ecological communities should therefore be studied both in isolation and in concert (see next chapter). Importantly, dead shells were common on sediment surfaces in all estuaries, suggesting that shells may have an important, yet understudied, impact on other estuarine species (see also next chapter). Finally, I found an inverse relationship between the abundances of seaweed and seagrass, suggesting competition for limited resources. If estuaries in New Zealand become more eutrophied, a reduction in the extent of existing seagrass beds are therefore expected.

2.5. Figures

Figure 2.5.1. Study 1: Close-up survey across latitudes – distribution and abundances
Mean percent cover (± 95% confidence intervals) of A) Shells, B) *Zostera*, C) *Ulva*, D) Mud, and D) Rocks in nine estuaries that represent three latitudinal regions (North, Central, South) and three levels of anthropogenic stress (Low, Moderate, High). See method section for details of each estuary.

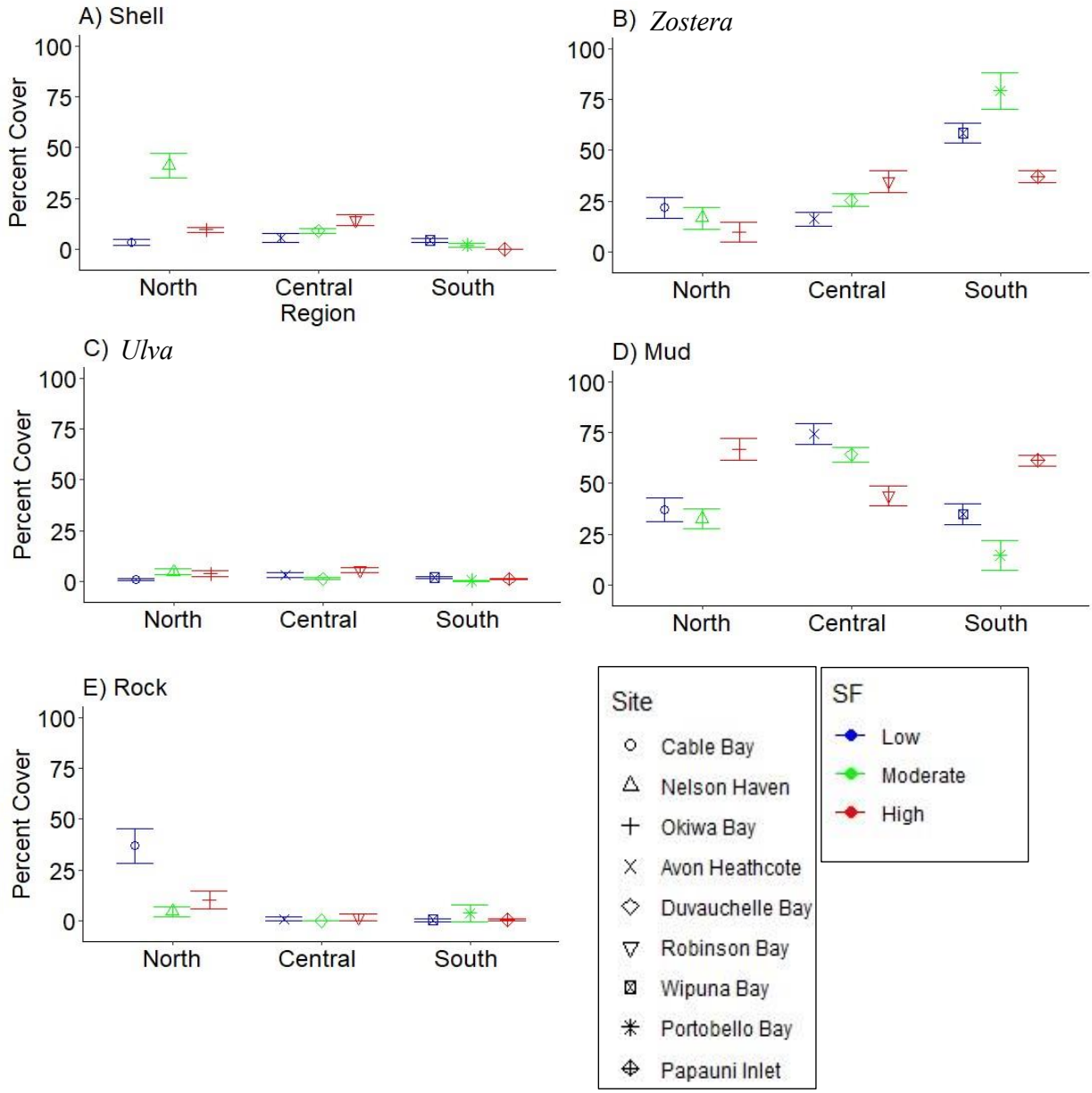


Figure 2.5.2. Study 1: Close-up survey across latitudes – correlations
Correlation between percent cover of A) *Zostera* vs *Ulva*, B) *Zostera* vs shells and C) *Ulva* vs shells. Individual samples are marked by latitudinal region and levels of anthropogenic stress.

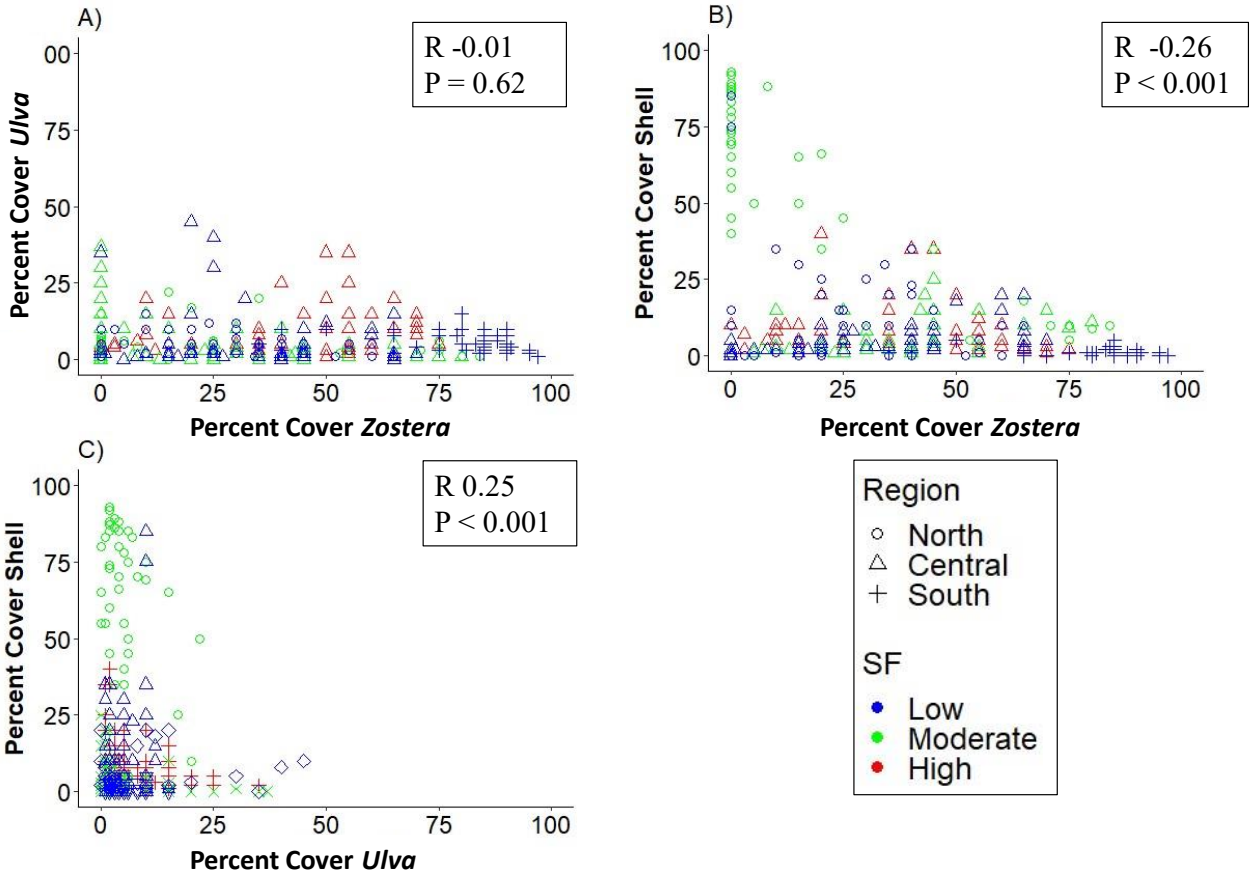


Figure 2.5.3. Study 2: Landscape survey across latitudes – distribution and abundance
Mean percent cover (± 95% confidence intervals) of A) Shells, B) *Zostera*, C) *Ulva*, D) Mud, and D) Rocks in nine estuaries that represent three latitudinal regions (North, Central, South) and three levels of anthropogenic stress (Low, Moderate, High). See method section for details of each estuary; Nelson Haven, Portobello Bay and Papanui inlet could not be sampled because of flight restrictions or poor weather conditions.

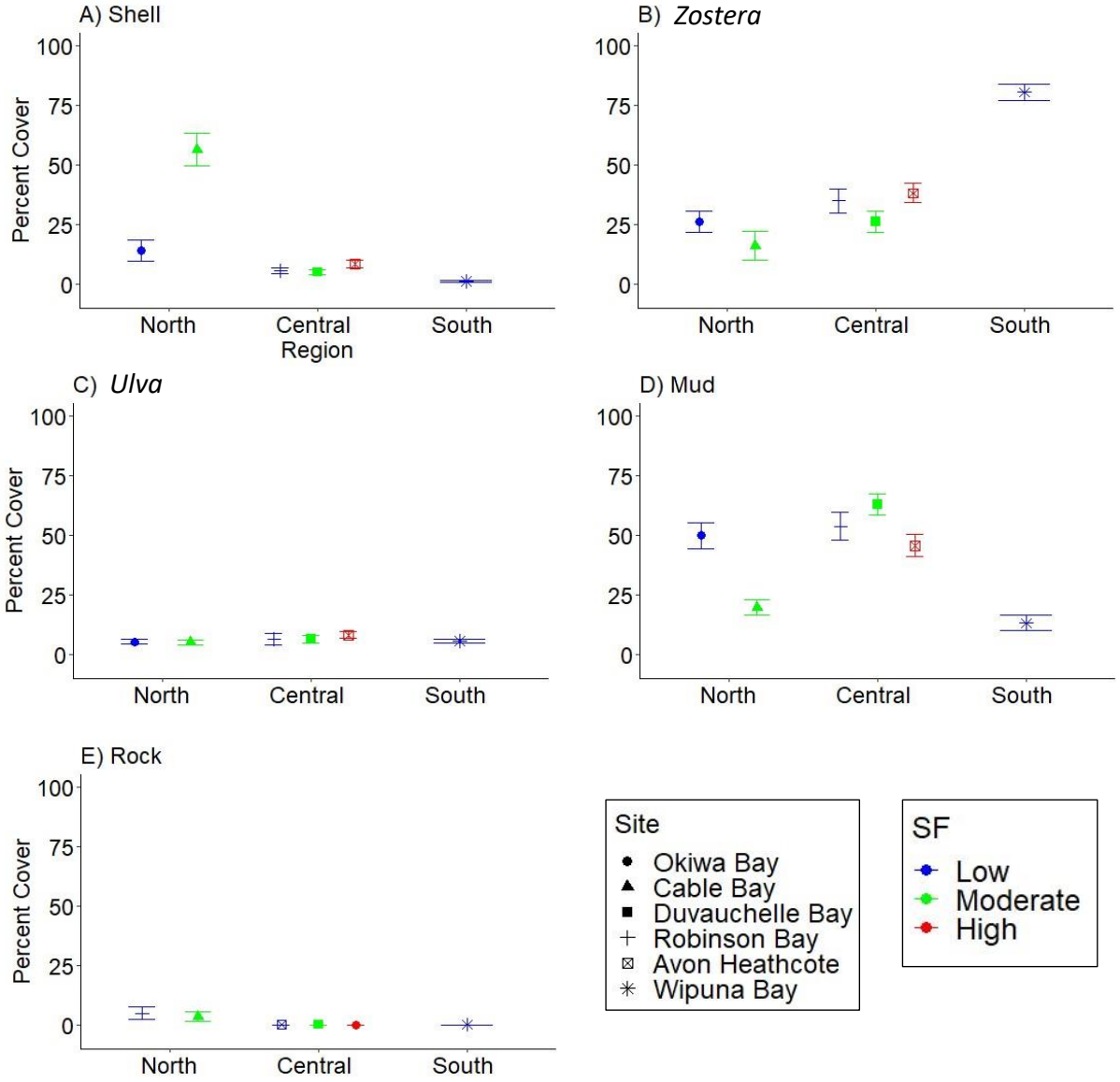


Figure 2.5.4. Study 2: Landscape survey across latitudes – correlations
Correlation between percent cover of A) *Zostera* vs *Ulva*, B) *Zostera* vs shells and C) *Ulva* vs shells. Individual samples are marked by latitudinal region and SF = Anthropogenic stress factor (Table 2.5.5).

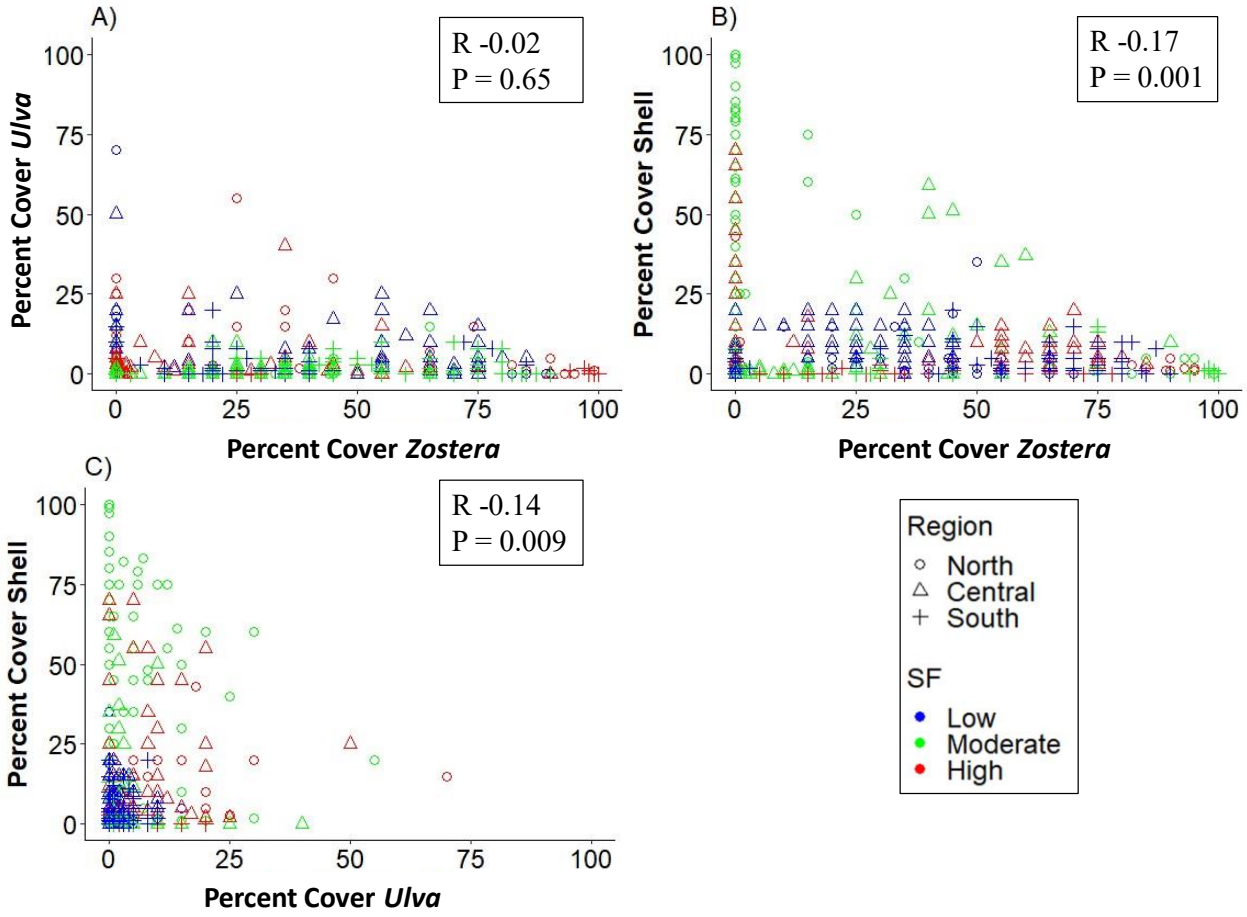


Figure 2.5.5. Study 3: Close-up survey across seasons – distribution and abundance
Mean percent cover (± 95% confidence intervals) of A) Shells, B) *Zostera*, C) *Ulva*, D) Mud, and D) Rocks in the Avon Heathcote Estuary in summer and winter.

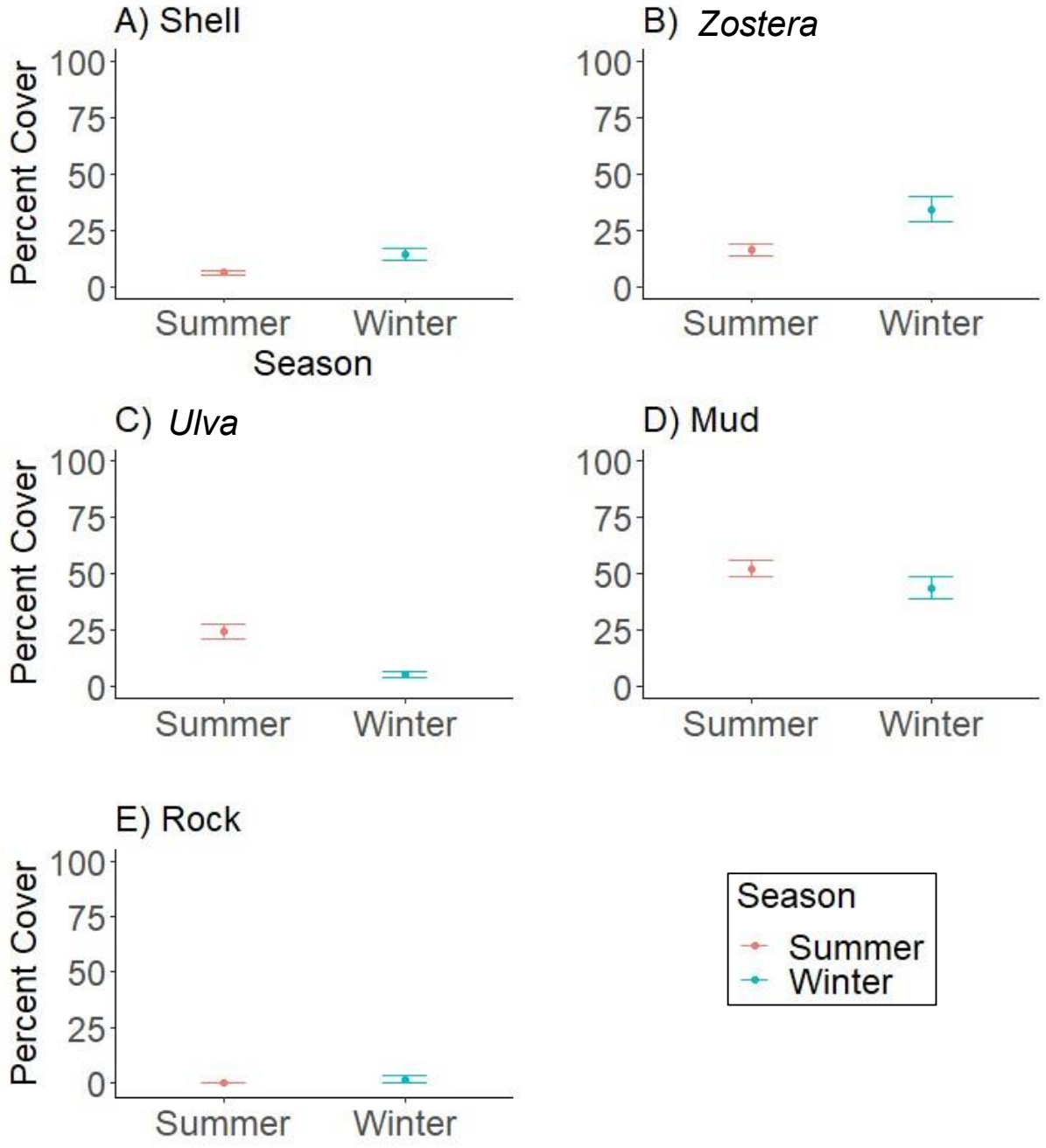


Figure 2.5.6. Study 3: Close-up survey across seasons - correlations
Correlation between percent cover of A) *Zostera* vs *Ulva*, B) *Zostera* vs shells and C) *Ulva* vs shells. Individual samples are marked by season.

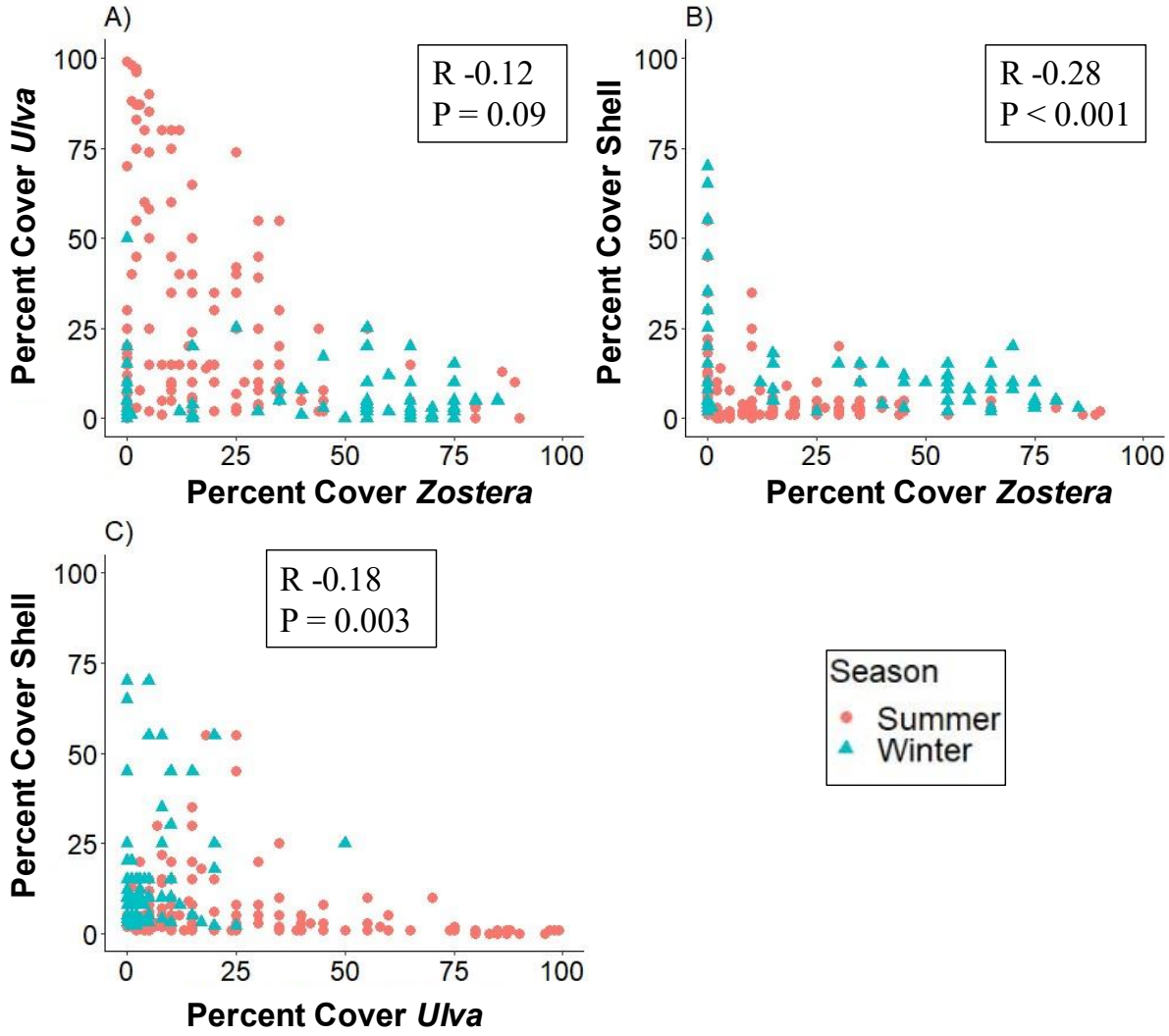


Figure 2.5.7. Study 4: Landscape survey across seasons – distribution and abundance
Mean percent cover (± 95% confidence intervals) of A) Shells, B) *Zostera*, C) *Ulva*, D) Mud, and D) Rocks in the Avon Heathcote Estuary at two sites across seasons.

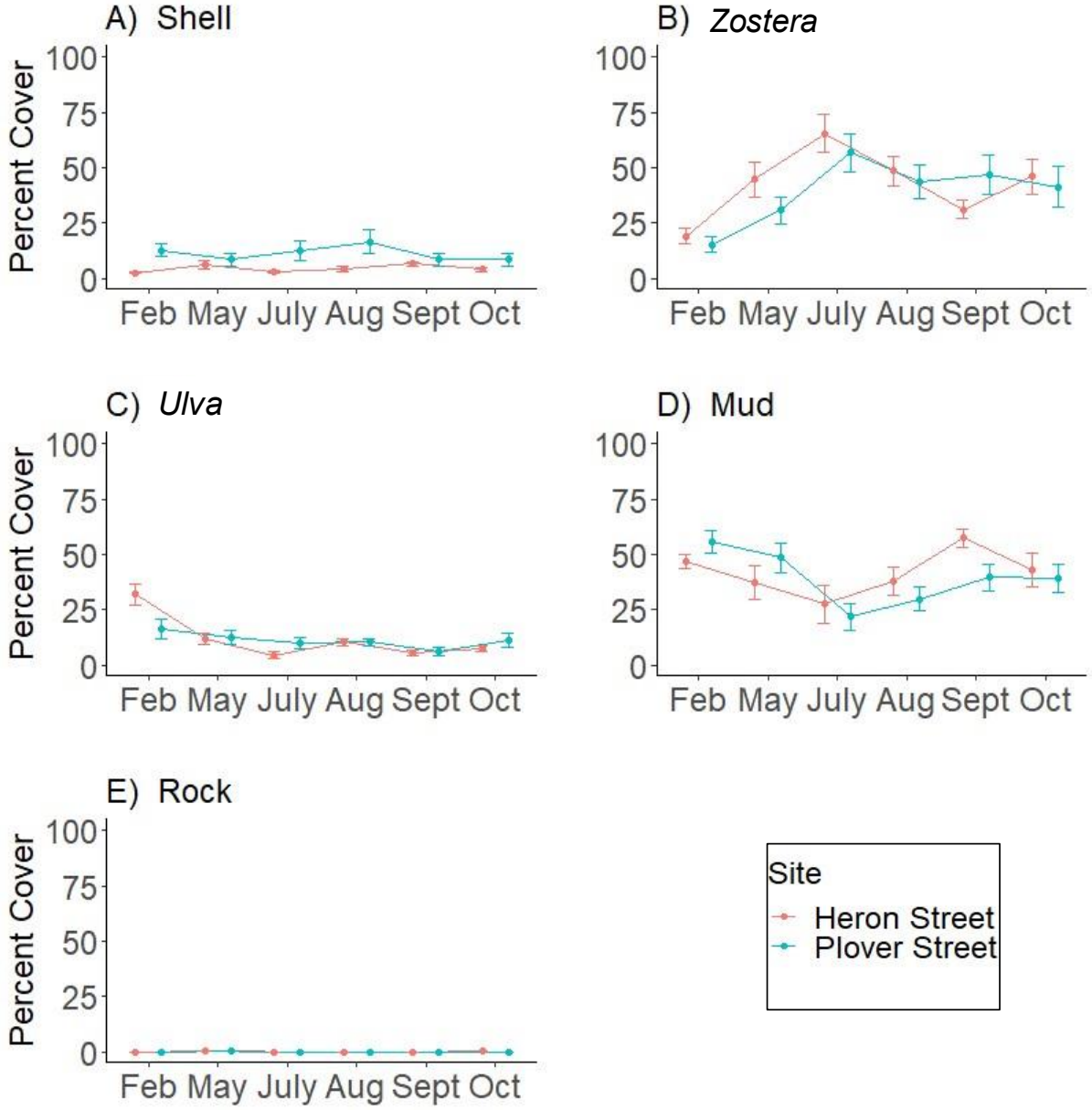
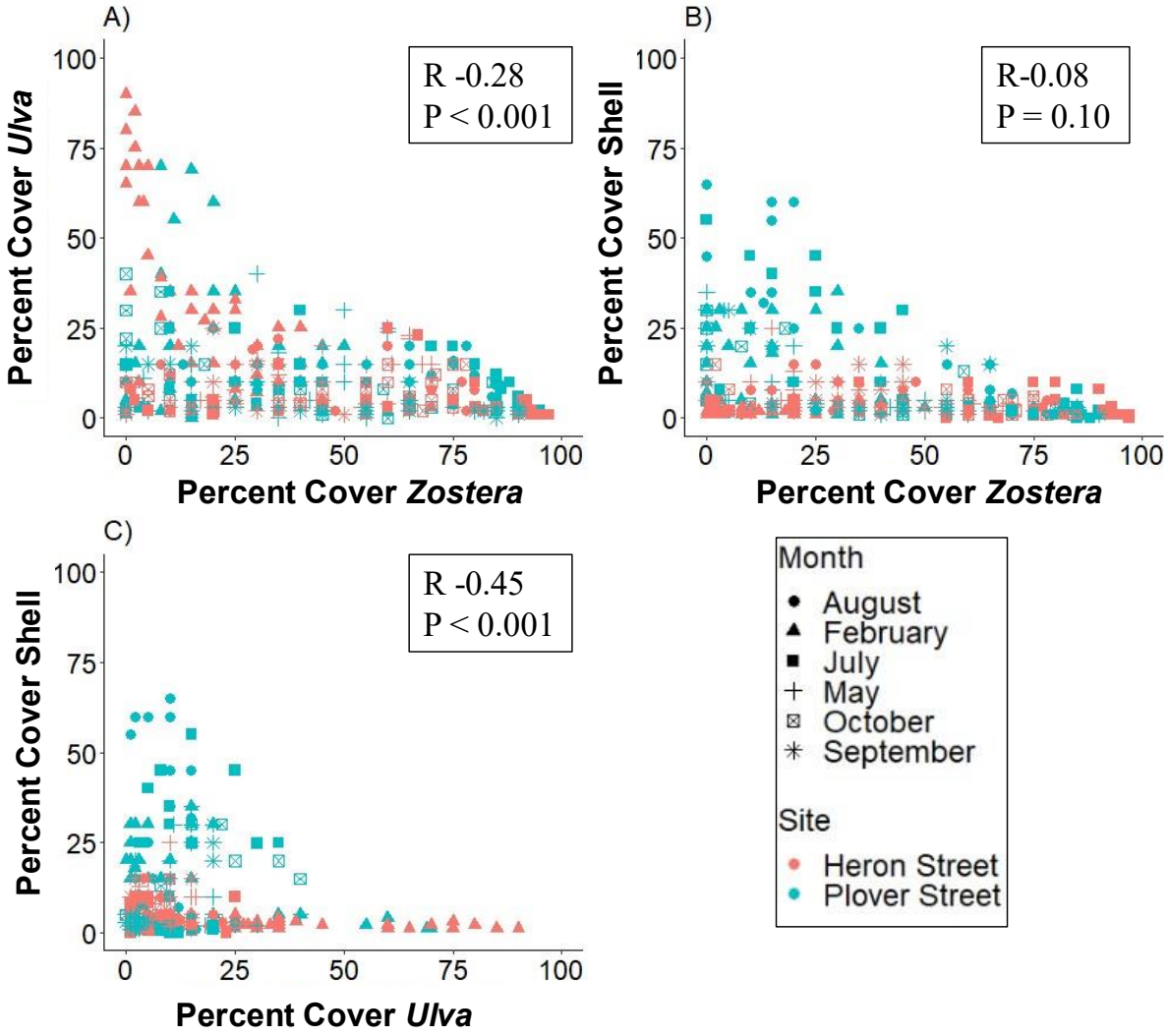


Figure 2.5.8. Study 4: Landscape survey across seasons – correlations
Correlation between percent cover of A) *Zostera* vs *Ulva*, B) *Zostera* vs shells and C) *Ulva* vs shells. Individual samples are marked by month and site.



2.7. Tables

Table 2.7.1. Study 1: Close-up survey across latitudes – distribution and abundances
Two-way ANOVA testing the effects of latitudinal region (North n = 237, Central n = 237, South n = 244) and anthropogenic stress level (Low, Moderate, High) on arcsine transformed percent cover of (A) shells, (B) *Zostera*, and (C) *Ulva*. Significant p-values are in bold.

Response	Test Factor	Df	SS	F	P
(A) Shell	Latitude	2	4.954	81.39	< **0.001**
	Stress	2	3.762	61.82	< **0.001**
	Latitude × Stress	4	6.058	49.77	< **0.001**
	Residuals	709	21.58		
(B) *Zostera*	Latitude	2	21.45	119.2	< **0.001**
	Stress	2	3.85	21.38	< **0.001**
	Latitude × Stress	4	14.00	38.91	< **0.001**
	Residuals	709	63.80		
(C) *Ulva*	Latitude	2	0.081	10.255	< **0.001**
	Stress	2	0.023	2.97	0.052
	Latitude ×Stress	4	0.109	6.923	< **0.001**
	Residuals	709	2.784		

Table 2.7.2. Study 2: Landscape survey across latitudes – distribution and abundance
One-way ANOVA testing for effect of latitudinal region (North n = 47, Central n = 49, South n = 47 – only using data from estuaries with low anthropogenic stress) on arcsine transformed cover of (A) shells, (B) *Zostera*, and (C) *Ulva*. Significant P-values are in bold.

Response	**Test Factor**	**Df**	**SS**	**F**	**P**
(A) Shell	Latitude	2	0.454	15.86	< **0.001**
	Residuals	140	2.004		
(B) *Zostera*	Latitude	2	13.405	138.6	< **0.001**
	Residuals	140	6.771		
(C) *Ulva*	Latitude	2	0.003	0.332	0.718
	Residuals	140	0.670		

Table 2.7.3. Study 2: Landscape survey across latitudes – distribution and abundance Two-way ANOVA testing for effects of latitudinal region (northern estuaries = Cable Bay and Okiwa Bay; n = 96, central estuaries = Robinsons Bay and Duvauchelle Bay; n = 129) and anthropogenic stress (Low, Moderate) on arcsine transformed cover of (A) shells, (B) *Zostera*, and (C) *Ulva*. Significant P-values are in bold.

Response	**Test Factor**	**Df**	**SS**	**F**	**P**
(A) Shell	Latitude	1	6.668	173.78	< **0.001**
	Stress	1	2.496	65.04	< **0.001**
	Latitude × Stress	1	3.384	88.19	< **0.001**
	Residuals	221	8.48		
(B) *Zostera*	Latitude	1	0.43	6.835	**0.009**
	Stress	1	0.49	7.79	**0.006**
	Latitude × Stress	1	0	0.002	0.961
	Residuals	221	13.77		
(C) *Ulva*	Latitude	1	0.010	1.435	0.232
	Stress	1	0.000	0.02	0.879
	Latitude × Stress	1	0.000	0.032	0.858
	Residuals	221	1.475		

Table 2.7.4. Study 4: Landscape survey across seasons – distribution and abundance
One-way ANOVA testing for effects of season (months) on arcsine transformed percent cover of A) *Zostera*, (B) *Ulva*, and (C) shells. Significant P-values are in bold.

Response	Test Factor	Df	SS	F	P
(A) Shell	Months	5	0.111	1.721	0.128
	Residuals	429	5.545		
(B) *Zostera*	Months	5	14.26	32.06	< **0.001**
	Residuals	429	38.17		
(C) *Ulva*	Months	5	2.749	27.16	< **0.001**
	Residuals	429	47.3		

Chapter 3. Variability in habitat usage by estuarine invertebrates across temperature-related spatiotemporal gradients

3.1. Introduction

Estuarine ecosystems bridge the land and the sea and provide a range of diverse habitats and ecosystem services, locally, regionally, and globally (Elliott et al. 2007, Barbier et al. 2011, Savage et al. 2012). Like in terrestrial, freshwater, and marine ecosystems, estuarine species that build biogenic habitat (i.e., habitat-formers and foundation species) are also important contributors to ecosystem productivity and many other ecosystem functions (Ellison et al. 2005, Thomsen et al. 2010a, Angelini et al. 2011, Ellison 2019). For example, habitat-forming species can attenuate waves, ameliorate abiotic stress, filter land-derived runoffs, and take up nutrients (Turner et al. 2007, Angelini et al. 2011, Fraser et al. 2014, Cheng et al. 2015). Most habitat-forming species are sessile organisms, are abundant, and alter local abiotic environments (Dayton 1975, Ellison et al. 2005, Thomsen et al. 2010a). Examples of ecologically important marine habitat-formers include kelps, oysters, coral reefs, saltmarshes, mangroves, and seagrasses (Thomsen et al. 2010a, Angelini et al. 2011, Ellison 2019). It is imperative to understand how these organisms affect biodiversity and how their associated biodiversity will be affected by future anthropogenic stressors, such as climate changes and heatwaves (Ellison et al. 2005, Jentsch et al. 2007, Fraser et al. 2014, Cheng et al. 2015, Thomson et al. 2015, Bible et al. 2017).

In estuaries, seagrasses are among the most important habitat-formers that can provide many ecosystem services while also enduring intense anthropogenic pressures, like nutrient runoffs (Turner 1996, Turner and Schwarz 2006, Turner 2007), species invasion (Orth et al. 2006, Wernberg et al. 2011a, Dijkstra et al. 2012, Massa et al. 2013, Thomsen et al. 2013), rising sea surface temperatures (Madeira et al. 2012, Hughes et al. 2018), and increased frequency and duration of heatwaves (Thomson et al. 2015, Oliver et al. 2018a, Kendrick et al. 2019). Anthropogenic stressors can negatively impact seagrass habitats by limiting growth rates (O'Mara and Wong 2016), reproductive success (Eads et al. 2016, Armstrong et al. 2020), altering grazing rates of the seagrass or its epiphytes (Tomas et al. 2015), resulting in loss of entire seagrass beds (Orth et al. 2006, Short et al. 2014), ecosystem services (Orth et al. 2006, Turner et al. 2007), and suitable physical habitat (Tomlinson and Posluzny 2001, Waycott et al. 2009, Smale et al. 2017, Wild et al. 2019). Furthermore, anthropogenic stressors, such as excess nutrients, may exacerbate effects from warming (Diaz et al. 2008, Cheng et al. 2015).

The ecological performance of seagrass is directly affected by high temperature (Bulthuis 1987, Koch et al. 2007, Lee et al. 2007, Höffle et al. 2012). For example, Höffle et al. (2012) found that the seagrass *Halophila ovalis* had reduced above-ground biomass, below-ground biomass and shoot length when exposed to multiple stressors associated with high temperature, drift algae and grazing rates. Elevated temperatures can increase metabolic demand in seagrasses resulting in lowered oxygen availability and disrupting other biogeochemical process within the plant (Borum et al. 2005, Koch et al. 2007, Höffle et al. 2012).

Anthropogenic stressors not only affect the seagrasses themselves but also the ecological communities that depend on them (Boström et al. 2006, Tomas et al. 2015). For example, small temperature increases can change physiological function and the ontogeny of estuarine invertebrates (Pörtner and Knust 2007, Rosenzweig et al. 2008) and effects from localized hypoxia often increase when high temperatures are combined with excess nutrients (Vaquer-Sunyer and Duarte 2011). However, it is not fully understood how co-occurring stressors (e.g., elevated temperature, hypoxia, and excessive nutrients) will impact estuarine communities across spatiotemporal scales (Harley et al. 2006). A dramatic example of seagrass loss was documented following an extreme marine heatwave in 2010/2011 in Shark Bay, Western Australia (Fraser et al. 2014, Thomson et al. 2015). This world heritage site lost up to 58% of its seagrass beds, with cascading negative impacts on commercially important species like roe abalone (*Haliotis roei*, with a 99% mortality on juveniles) (Hart 2014) and western rock lobster (*Panulirus cygnus*) (Smale et al. 2017). For some seagrass-associated animals, recovery took up to seven years, and that included supplementing the natural population (abalone) with aquaculture reared individuals (Caputi et al. 2019, Strain 2019).

Globally, effects of temperature, warming, and heatwaves have been studied in many seagrass systems (Smale et al. 2019) but this information is largely lacking from seagrass beds in New Zealand, where studies mainly have focused on local populations (Ismail 2002, Hume et al. 2007, Anderson et al. 2017, Dos Santos and Matheson 2017, Berthelsen et al. 2018). Furthermore, even less is known about how seagrass-associated animals in New Zealand are affected by temperature related stressors. Analysing the effects of future changes to temperature, heatwaves, or other anthropogenic stressors on seagrass-associated communities in New Zealand will require rigorous baseline data collected across spatiotemporal gradients, including latitudes, estuaries, locations, elevation levels and seasons (Levin 1992). However, such multifactorial data about seagrass-associated

invertebrates are missing from the South Island of New Zealand. *The general objective of this chapter is to address this research gap by collecting and analysing multifactorial seagrass-associated invertebrate data from the South Island of New Zealand.*

Collecting robust data targeted to test for future elevated temperature stress can be done with time-for-space substitution surveys along latitudinal or elevational stress gradients (Pickett 1989, Wernberg et al. 2010a, Lester et al. 2014, Damgaard 2019) and time-for-time substitution across seasons (Blois et al. 2013, Elmendorf et al. 2015). Data collected along these gradients are also important because impacts from heatwaves, for example, depend on whether they occur toward the equatorial (warm conditions) or poleward (cold conditions) ranges of a species' distribution, or in summer (warm conditions) or winter (cold conditions) (Wernberg et al. 2016, Wernberg et al. 2018, Smale et al. 2019). Similarly, temperature effects can also vary along elevation gradients. For example, deep water can provide cold refugia (Graham et al. 2007, Wernberg et al. 2011b), and intertidal organisms experience greater desiccation and temperature stress at higher elevations (Raffaelli and Hawkins 2012, Thomsen et al. 2019a). In other words, to understand present distribution patterns and future-proof anthropogenic impact analyses, baseline data should capture these spatiotemporal gradients.

Most studies on habitat-forming estuarine species have compared seagrasses to adjacent unvegetated areas ('bare' areas dominated by mud or sand) (Boström et al. 2006). However, other estuarine habitat-formers may provide similar ecological functions to seagrasses. Other estuarine habitat-formers include mussel beds (Dame et al. 1991), oyster reefs (Zimmerman et al. 1989, Thomsen and McGlathery 2006), polychaete gardens (Thomsen and McGlathery 2005, Kollars et al. 2016), seaweed beds (Thomsen et al. 2006, Lyons et al. 2014, Thomsen et al. 2019b), and unconsolidated and scattered (alive or dead) bivalve shells (Thomsen et al. 2016, Foster 2019). It is largely unknown how common these 'alternative' (to seagrass) foundation species (Thomsen and South 2019) are in estuaries on the South Island of New Zealand and what their ecological roles are. *The specific objective of this chapter is therefore to compare the distributions and abundances of estuarine animals across latitudes, elevations, and seasons associated with different types of habitats including bare mudflats, seagrasses, seaweed and scattered dead shells*. For simplicity, I focus the analyses on three fundamental biodiversity responses: the number of individuals in a sample (total abundance), the number of taxa in a sample (richness), and the multivariate community structure of a sample (Clarke 1993).

Foundation species typically co-occur in coastal marine ecosystems, where interactions between bivalves, gastropods and seaweeds creates a mosaic of habitats comprised of primary habitat formers (e.g. seagrasses) (Angelini et al. 2011, Thomsen et al. 2018b, Ellison 2019) and alternative habitat formers (Thomsen et al. 2016, Thomsen et al. 2018b, Thomsen and South 2019) that coexist as a part of different species assemblages. The coexistence of primary and alternative habitat formers is comprised of adjacent or nested assemblages (Angelini et al. 2011, Thomsen et al. 2016, Thomsen and South 2019). Adjacent assemblages are densely distributed primary foundation species, generally across a landscape scale, that leaves no additional space for alternative foundation species to occupy (Angelini et al. 2011). In contrast, nested assemblages are foundation species that co-occur in the same area, whether due to primary foundation species not occupying entire space or providing suitable habitat for the colonization of local area by alternative foundation species (Angelini et al. 2011). Of most interest to this study are nested assemblages, as these types of species assemblages take into account a greater number of foundation species per sampling event (Foster 2019).

To address the general and specific study objectives, I quantified the distribution, abundance, community structure (based on core data) and the number and types of habitat-interactions between estuarine organisms (based on quadrat data), with supplementary methods along both a latitudinal and seasonal gradient. More specifically, quadrat sampling quantified fine-scale epifaunal habitat-interactions, whereas core sampling quantified general habitat-associations that included infauna, buried shells, and below ground seagrass roots and rhizomes.

3.2. Methods

3.2.1. Study locations and study organisms

For the latitudinal study, 9 estuaries were sampled on the South Island, including three northern (Nelson Haven at -41.2361 S, 173.316 E, Cable Bay at -41.1688 S, 173.442032 E, Okiwa Bay at –41.2645 S, 173.916763 E), three central (Avon Heathcote at -43.549 S, 172.746 E, Duvauchelle Bay at -43.752 S, 172.927 E, Robinsons Bay at -43.763 S, 172.960 E) and three southern (Papanui Inlet at -45.8389 S, 170.692 E, Portobello Bay at -45.8304 S, 170.672 E, Waipuna Bay at -45.7875 S, 170.67 E) estuaries. Northern estuaries were sampled

from June 1-5, central estuaries from September 3-11, and the southern estuaries from July 22-26, all in 2020. For the seasonal study, two of the three central estuaries were sampled repeatedly through time; The Avon Heathcote Estuary was sampled monthly between November 2019 and October 2020 and Duvauchelle Bay was sampled monthly between December 2019 and October 2020. The estuaries are described in more detail in Chapter one, including their 'human-impact' level or anthropogenic stress classification, where each latitudinal region is represented by a high, moderate, and relatively low impact-level estuary (see Table 1.8.1. for estuary 'Anthropogenic Stress' classification).

3.2.2. Latitudinal survey: Quadrats

Quadrats (0.010 m^2) were sampled from the nine estuaries described above during daylight hours at low tide. Within each estuary, 12 quadrates were sampled, matching geocoordinates described in Foster (2019). Each quadrat was located with Google Maps on an iPhone within ca. 5 m of previously reported geocoordinates. Six quadrats were respectively sampled in the intertidal-subtidal transition zone and in the higher shore (>10 m away) Note that due to bad weather, only two high elevation quadrats were sampled from Okiwa Bay. A digital geotagged photo was taken perpendicular to the substrate (i.e., to each quadrat, using Nikon CoolPix AW130). Percent cover of the dominant habitat types was estimated from each photo. The dominant habitat types quantified were the percent cover of dead shells, seagrass, seaweed, and abiotic substrates (rock or mud). This method does not consider the possibility of layering of habitat types, so if the entire quadrat was covered by a dense seaweed mat, then only the seaweed was recorded. In the field, the numbers, and species identities of all 'habitat-interactions' visible to the naked eye were identified and tallied. Here, habitat-interactions refer to the type of habitat a species was found on or under - including the top 1 cm of the sediment surface. For example, if *Anthopleura aureoradiata* was found attached to *Austrovenus stutchburyi* this was tallied as one habitat-interaction. Habitat-interactions for sessile and strongly attached habitat-users were straightforward to quantify because these habitat-users were always physically attached to a habitat-former (e.g., limpets-attached-to-dead shells, barnacles-attached-to-cockles). By comparison, habitat-interactions for mobile organisms also included interactions observed underneath structures, such as crabs-under-dead-shells, or snails-under-drift-algae.

3.2.3. Latitudinal survey: Cores

Cores (9 cm inner diameter, collected to 10 cm depth = 0.0064 m^2) were collected from the same 9 estuaries during daylight hours at low tide. Three replicate core samples were collected from the mid-intertidal and intertidal-subtidal transition zones at random from each of four habitat types - bare sediment, sediment dominated by seaweed, sediment dominated by seagrass, and sediment that included seagrass and seaweed. A total of 216 cores were collected for this survey (9 estuaries × 4 habitats × 2 elevations × 3 replicates). Individual cores were placed in 1 mm mesh bags with labels and tied off with rubber bands. Mesh bags were rinsed in the field to remove most sediments and then stored at -20 °C until processing. Frozen samples were defrosted and rinsed with freshwater in a 1 mm sieve to remove the remaining sediments. The content of the mesh bag was placed in a sorting tray. Animals were separated and recorded to species level (most crustaceans and molluscs) or operational taxonomic units (fragmented/broken worms and small juvenile crabs), counted, and stored in 70% ethanol. Seagrass, seaweed, dead whole or fragmented shells larger than 10 mm were separated, and weights recorded after drying at 70°C for 72 hours. Sieving in the field and lab and freeze-thawing fragmented and broke soft and fragile invertebrates (like anemones and worms) so data for these organisms are less reliable (in other words, the analysis of core data focus primarily on organisms with hard external shells).

3.2.4. Seasonal survey: Quadrats

In the Avon-Heathcote, 60 quadrates covering 9 locations were sampled for detailed habitat-association between foundation species and ecological communities each month during spring tides. The same methods were used as described for the latitudinal quadrat survey except I here used a larger 0.0625 m^2 quadrat because the 9 locations had easier access and I could (in contrast to the latitudinal survey) revisit locations over multiple sampling dates. Half of the quadrates were from the mid-tidal zone and half from the intertidal-subtidal transition zone. Like for the latitudinal survey, each quadrate was located with Google Maps on an iPhone. Individual quadrats were sampled haphazardly within five meters of the geo-referenced area. In Duvauchelle Bay**,** 24 quadrates were sampled monthly - 12 quadrats from the mid-tidal zone and 12 from the intertidal-subtidal transition zone. All response variables were measured as described for the latitudinal survey.

3.2.5. Seasonal survey: Cores

Seasonal sampling consisted of taking three replicated 0.0064 m^2 circular cores from both the subtidal/intertidal transition zones and the mid-intertidal zones at two locations (Plover street at -43.549467 S, 172.743438 E vs. Tern street at -43.5527 S, 172.7451 E) in the Avon Heathcote estuary. Cores were 10 cm deep and collected from bare sediment, sediment covered in seaweed, sediment covered in seagrass, and sediment covered with co-occurring seagrass and seaweed as was done for the latitudinal survey. Sampling was done in summer (February 2020) and winter (July 2020) corresponding to a total of 48 cores (4 habitats × 2 elevations × 2 seasons × 3 replicates). Cores were processed as described in the latitudinal survey.

3.2.6. Statistical analysis

Cover data of habitat-forming organisms from the latitudinal and seasonal quadrat surveys were analysed graphically (their distribution and abundances are analysed statistically in chapter 2), whereas invertebrate data were analysed with permutation based factorial ANOVAs on univariate responses (abundances, richness) and permutation based factorial MANOVAs on multivariate community structure. Response variables from the quadrats included (a) total number of habitat-interactions recorded per quadrat (analogous to total abundances in a sample), (b) the number of unique habitat-interactions per quadrat (analogous to richness of a sample) and (c) the full sample-habitat-interactions matrix (analogous to multivariate community structure of a sample). The latitudinal invertebrate data from quadrats were analysed with fixed 3-factorial (M)ANOVAs, testing for orthogonal effects between latitude (north, central, south), tidal elevation (high, low), and anthropogenic impacts (low, moderate, high). For the seasonal data I first show monthly changes in the same three response variables (i.e., abundance, richness, multivariate community structure), followed by fixed 3-way factorial (M)ANOVA testing for orthogonal effects of season (where monthly data were classified into 6 coldest (May-September) vs. 6 warmest (October-March) months), tidal elevation (high, low) and estuary (Avon-Heathcote, Duvauchelle Bay). Estuary was considered a fixed factor because the Avon Heathcote estuary represented a highly modified estuary surrounded by a large city whereas Duvauchelle Bay represented a less modified estuary surrounded by livestock farming.

Response variables for the analyses of core data were (a) total organismal abundances , (b) taxonomic richness and (c) multivariate community structure (Clarke 1993). The latitudinal

core data were analysed with 4-factorial fixed (M)ANOVAs testing for orthogonal effects of latitudinal region (north, central, south), tidal elevation (high, low), seaweeds (presence, absence) and seagrass (presence, absence). Finally, seasonal core data were also analysed with 4-factorial fixed (M)ANOVAs testing for orthogonal effects of season (summer, winter), elevation (high, low), seaweed (presence, absence), and seagrass (presence, absence). Homogeneity of variances were checked using Levine's test in UNISTAT®. If data failed Levine's test, data were square root transformed and rechecked. Significant effects were evaluated at $p = 0.05$. For multivariate analyses, Bray-Curtis similarity matrices were constructed (with a dummy variable of $n = 1$) from square root transformed data with 4999 permutation. Principal coordinate analysis (PCO) with vector overlay correlations set at 0.25, were also constructed from the Bray-Curtis similarity matrix. All analyses (minus Levine's test) were done in PRIMER 6 (using Euclidean distances for univariate responses) (Clarke and Gorley 2015). All figures with the expectation PCO plots were made in R (Team 2020) and were produced using the package ggplot2 (Wickham 2016).

3.3. Results

3.3.1. Latitudinal survey: Quadrats

3.3.1.1. Latitudinal survey: Quadrats - cover types

Cover of habitat-formers was variable across latitudes and elevations (Fig. 3.5.1.1). The greatest difference across latitudes was observed for seagrass, which was most abundant in the southern region. Cover of dead shells on the sediment surface was also variable across regions and tended to be most abundant at lower elevation. Seaweeds were generally most abundant at low elevation at the central estuaries, although at the northern estuaries, seaweed were more abundant at higher elevations. Rock cover was generally low across regions with highest cover at the northern high elevation levels.

3.3.1.2. Latitudinal survey: Quadrats - habitat-interactions

There were significant effects on the mean number of habitat-interactions from region × elevation × impact ($p = 0.029$), region × impact ($p < 0.001$), and elevation ($p = 0.029$, Table 3.6.1A). The mean number of habitat-interactions per sample was highest at central low elevation levels (8.56 ± 2.20) and lowest in southern high elevation levels (2.33 ± 0.71, Fig. 3.5.1.2.A). Results were relatively similar for richness of habitat-interactions (region × elevation × impact, $p = 0.023$; region × impact, $p < 0.001$), but there were no significant

single factor effects (Table 3.6.1B). Richness of habitat-interactions was greatest at northern low elevation levels (9.00 ± 0.65), and lowest at southern high elevation levels (5.00 ± 2.24, Fig. 3.5.1.2B). Finally, effect on community structures were significant for region × elevation × stress ($p < 0.001$), region × stress ($p < 0.001$), region × elevation ($p = 0.038$) and region ($p < 0.001$, Table 3.6.1C). Graphical analysis of the PCO plot (Fig. 3.5.1.3) showed that northern high and low elevation levels generally were grouped together, and central and southern regions (irrespective of elevation levels) were relatively similar. The community pattern of habitat-interactions was driven by *Austrovenus* inhabiting mud and dead shells as habitat formers driving differences between elevation, latitude, and human impacts.

3.3.2. Latitudinal survey: Cores

The abundance of habitat-users in the core samples was significantly affected by latitude × elevation ($p = 0.012$), seaweed ($p < 0.001$) and elevation ($p < 0.001$, Table 3.6.2.A, Fig. 3.5.2.1.A). Cores with both seagrass and seaweed had greatest mean abundance at central low elevations (12.0 ± 12.54). High abundances of habitat-users were also found at low elevations across latitudes in cores dominated by seagrass, with greatest abundances at southern low elevation levels (8.00 ± 5.44). Seagrass also had the highest single value for individual invertebrate abundance (372 individuals in a core). Mean abundances in cores dominated by seaweed was greatest at southern low elevation levels (10.29 ± 8.16) and the second highest number of individuals (311) was found in this habitat.

Taxonomic richness was affected by seagrass × elevation × latitude ($p = 0.015$), elevation × latitude ($p = 0.036$), seaweed ($p = 0.001$), elevation ($p = 0.005$), and latitude ($p = 0.001$, Table 3.6.2B). Seaweed cores at central high elevation levels had highest richness (3.47 ± 1.16, Fig. 3.5.2.1B). Bare mud cores generally had low richness peaking at the central low elevation level (1.44 ± 1.23), with more variable richness at the northern regions but relatively similar richness across the southern regions. Richness in cores dominated by seagrass were relatively similar across regions and elevations (northern: 2.00 ± 0.67, central: 1.33 ± 1.21, southern: 1.5 ± 1.21). Cores dominated by seaweed had highest richness of any habitat type (3.46 ± 1.16), but there was also high variation between elevations in central and southern regions. By comparison, cores with co-occurring seagrass and seaweed had similar richness at northern high elevation (2.00 ± 0.87) and southern low elevation (2.00 ± 0.67) levels.

The multivariate community structure was significantly affected by latitude × elevation ($p < 0.001$), seagrass ($p = 0.002$), seaweed ($p < 0.001$), elevation ($p < 0.001$), and latitude ($p < 0.001$) (Table 3.6.2C). Graphical analysis of the PCO plot (Fig. 3.5.2.2) showed large overlay between central and northern regions with southern region sample clusters being more affected by elevation than other regions. Vector overlays were dominated by *Micrelenchus tenebrosus,* sedentaria polychaetes and *Zeacumantus subcarinatus* where the former species was equally distributed between regions whereas the latter two taxa were more important in southern regions.

3.3.3. Seasonal survey: Quadrats

3.3.3.1. Seasonal survey: Quadrats – cover types

In the Avon-Heathcote cover types varied slightly across seasons with greater variation between low and high elevations than across months (Fig. 3.5.3.1A). Rocks were rare – only being recorded at high elevations in November 2019. Mud cover was greatest at high elevations in May (77.0%) and lowest in March at low elevation (62.2%). Seaweed cover was generally greater at lower elevations but was relatively stable between March-October 2020. Greatest cover was observed in February 2020 at low elevations (20.6%) and lowest cover in October at high elevation (7.42%). Seagrass cover followed similar patterns with greater cover at lower elevations with lowest cover in February (2.8%) and highest cover in October (11.8%). Dead shell cover was greatest in November 2019 (15.5%) and lowest in September 2020 at high elevations (6.0%).

In Duvauchelle Bay, seagrass cover was higher compared to the Avon Heathcote estuary, whereas cover of seaweed and dead shells were lower (Fig. 3.5.3.1B). Cover of rocks did not show any directional trend and had greatest cover in July at high elevation (5.6 %). Duvauchelle Bay had higher cover of bare mud than the Avon Heathcote estuary, with the largest monthly cover found in March at high elevation (88%) and least cover in the same month at low elevations (36.4%). Seaweed cover was lower than in the Avon Heathcote estuary, and had highest cover in January at high elevation (5.9%), and with no seaweed at all in December March, May, and August. Seagrass cover was greatest in March at low elevations (63.0%) and lowest in January at high elevation (6.9%) but with no clear seasonal trends. Finally, cover of dead shells was greatest in July at high elevations (7.3%) and lowest in February at low elevations (0.10%).

3.3.3.2. Seasonal survey: Quadrats – habitat-interactions

Test results were similar for the number and richness of habitat-interactions with significant effects of elevation × estuary ($p < 0.001$), season × estuary ($p < 0.001$, season ($p < 0.001$), elevation ($p < 0.001$) and estuary ($p < 0.001$, Table 3.6.3A,B). The number and richness of interactions were generally much higher in the Avon Heathcote estuary than in Duvauchelle Bay (Fig. 3.5.3.2A,B). Furthermore, the number of habitat-interactions was greatest at lower elevations in winter (53.47 ± 4.49) at high elevations (20.67 ± 1.44, Fig. 3.5.3.2A). Duvauchelle Bay had greatest and lowest number of habitat-interactions in winter at high elevation (5.01 ± 0.48) and in summer at low elevation (2.33 ± 10.31), respectively. For the multivariate community data, all test factors were significant ($p < 0.001$, Table 3.6.3C) highlighting that each combination of test-factors had its own unique set of habitat-interactions. The PCO plot suggested effects of latitude and stress was greater than seasonal and elevation effects, i.e., there was greater separation of samples between latitude and stress (Fig. 3.5.3.3).

3.3.4. Seasonal survey: Cores

Invertebrate abundances were significantly affected by seagrass ($p = 0.014$), seaweed ($p < 0.001$), and season ($p = 0.038$) – but with no effect of elevation or any interactions (Table 3.6.4.A). Cores with bare mud had lowest abundances across habitat types, with the greatest abundance in the winter high elevation cores (0.82 ± 1.50, Fig. 3.5.4.1A). Cores dominated by seagrass had greater abundance at low elevations, with greatest abundance in the low elevation summer cores (2.03 ± 3.33). Cores dominated by seaweed had greater abundances at higher elevation in summer (4.03 ± 10.25), with opposite pattern in winter with higher abundances at lower elevations. Finally, the cores with both seagrass and seaweed had similar pattern as the cores with seaweed-only and had greatest abundances at low elevation (7.12 ± 13.58). The taxonomic richness of invertebrates was significantly affected by seagrass × elevation × season ($p = 0.005$), elevation × season ($p < 0.002$), and seagrass ($p = 0.001$), seaweed ($p < 0.001$), and season ($p < 0.016$, Table 3.5.4B). The cores with bare mud had lowest richness (2.00 ± 0.58, Fig. 3.5.4.1B) with slightly higher richness in summer. Seagrass dominated cores had highest richness in lower elevations during summer months (5.67 ± 1.42) whereas seaweed dominated cores had highest richness at high elevations independent of season (6.33 ± 0.33). Furthermore, the cores where seagrass and seaweed co-occurred had

similar high taxonomic richness at the high (3.00 ± 2.51) and low (3.00 ± 2.59) elevation level. However, during winter, more taxa were found at low elevation, including the greatest reported mean richness (4.33 ± 5.79) of any core type.

Finally, the multivariate community structure was significantly affected by seagrass × elevation × seaweed ($p = 0.007$), seagrass × seaweed ($p = 0.009$), seagrass × season ($p = 0.033$), elevation × season ($p = 0.020$), seagrass ($p = 0.003$), seaweed ($p < 0.001$), and season ($p = 0.024$, Table 3.6.4). Graphical analysis of PCO plot (Fig. 3.5.4.2) showed that cores with similar habitat type and elevation generally were clustered close to each other. Vector-overlays showed that *Micrelenchus tenebrosus* was driving much of the multivariate variability being most abundant in winter samples and in cores with seagrass and seaweed. By comparison, the bivalves *Macomona liliana* and *Paphies australis* were more abundant in summer and winter cores, respectively, but more so in mud-cores without vegetation.

3.4. Discussion

Research on organisms that depend on biogenic habitat (here referred to as 'habitat-users' – dominated by invertebrates but can include vertebrates and seaweeds) has typically concluded that seagrass is the most important organism that builds biogenic habitat in sedimentary estuaries (Orth et al. 1984, Boström et al. 2006, Battley et al. 2011, Juan and Hewitt 2011, Foster 2019). By companion, fewer studies have highlighted the importance of seaweeds (Lyons et al. 2014, Thomsen and Wernberg 2015, Ramus et al. 2017) or co-occurring habitat-formers – like seaweed entangled around seagrass leaves (Thomsen et al. 2010a). Here I documented that estuarine habitat-users can be strongly associated with other biogenic habitat formers such dead shells and cockles like *Austrovenus stutchburyi* in addition to being associated with seagrass and seaweed. Some studies have shown that poleward (cooler) climates have lower diversity of estuarine habitat-users (Duke et al. 1998, Engle and Summers 1999, Attrill et al. 2001) but I did not find that pattern in my surveys – species richness was generally similar across latitudes despite complex variability associated with specific combinations of habitat, estuaries and elevation levels – perhaps because the latitudinal gradient I sampled only spanned c. 5º latitude. The data collected here provides important baseline information about habitat-users across a range of latitudes, elevation, and seasons to gauge future impacts of climate changes and other human stressors.

3.4.1. Latitudinal survey: quadrat data

Considerable variation was found in the abundance of habitat-formers across latitude and elevations (Fig. 3.5.1). The cover of seagrass was most abundant at the southern latitude, a pattern commonly observed for *Zostera* spp. (Duke et al. 1998, Engle and Summers 1999, Attrill et al. 2001, Turner and Schwarz 2006). Cover of dead shells varied across regions, with higher cover at lower elevations, perhaps because stronger tidal currents and waves remove shells from this habitat (Olivera and Wood 1997). Seaweed cover was most prominent at low elevation central estuaries, partly driven by high cover in the Avon Heathcote estuary, a semi-enclosed shallow nutrient-rich estuary where mats of *Ulva* spp. and *Agarophyton chilensis* often accumulate (Marsden and Bressington 2009, Marsden and Maclaren 2010a, Thomsen et al. 2016). Regional differences in cover of foundation species may be explained by differences in environmental conditions (Turner 1996, Allison 2004, van Houte-Howes et al. 2004, Turner and Schwarz 2006), point source nutrient input and localized eutrophication (Turner 1996, Turner and Schwarz 2006, Turner 2007), or thermal

stress from air temperature and sea surface temperature (Ellis et al. 2017, Oliver et al. 2018b, Holbrook et al. 2019, Oliver 2019, Oliver et al. 2019).

The abundance, richness, and community structure of habitat-interactions was affected by latitude, elevation, and anthropogenic impacts with most habitat-interactions observed at low elevations (Fig. 3.5.2.1A). This pattern may be partly driven by higher densities of habitat-formers in this habitat (Fig.3.5.1), and partly by lower desiccation stress that relatively few species, like trochid snails and mud snails tolerate (Grant and McDonald 1979, Mitchell 1980, Shumway and Marsden 1982, Omori et al. 1998, Bertness et al. 2001, Jones et al. 2005). The most common habitat-interactions involved primary producers (*Zostera, Ulva, Agarophyton)* and different shell-producing molluscs, including gastropods (*Diloma*, *Micrelenchus tenebrosus*), limpets (*Notoacmea*), bivalves (*Austrovenus stutchburyi*) and dead-shells (Fig. 3.5.1.3). Indeed four of the 12 most important interactions were molluscs attached to dead shells, a habitat that is typically overlooked in estuarine studies (Gutiérrez et al. 2003, Foster 2019). Importantly, dead shell deposits, here mainly from *Austrovenus stutchburyi*, can provide habitat at a large scale (see Chapter two) across seasons, estuaries, and elevations (Grange 1979, Gagné et al. 2008, Summerhayes et al. 2009, Foster 2019). As different stressors can affect habitat-users and habitat-formers differently (Ellis et al. 2017), many habitat-users depend on shell aggerates and other biogenic habitats to find refuge from desiccation, elevated sedimentation and various anthropogenic stressors (Thomsen et al. 2016, Foster 2019). Loss of intertidal seagrass habitats (Turner 1996, van Houte-Howes et al. 2004, Turner and Schwarz 2006) may also have created more patches of bare substrate with elevated desiccation and thermal stress (Ellis et al. 2017). In these types of habitats, dead shells may now provide alternative stress-refugium during low tides.

3.4.2. Latitudinal survey: core data

Invertebrate habitat-users were generally more abundant and species rich at low elevations and associated with seaweeds as well as in cores with co-occurring seaweed and seagrass, but with no clear latitudinal patterns (Table 3.6.4, Fig. 3.5.2.1) - patterns that generally supported the habitat-interactions observed from the quadrat survey. These results are likely because more habitat-users can use transition zones between intertidal and subtidal habitats than stressful high intertidal elevations (Turner and Schwarz 2006, Turner 2007, Berthelsen et al. 2018) and because seaweed and seagrass provide food for grazers and ameliorate

environmental stress (Lyons et al. 2014, Thomsen et al. 2016). The most common seaweed, *Ulva* spp., requires hard substrate for its initial settlement and early growth (typically onto rocks, bivalves or dead shells) but often breaks and becomes drift algae that accumulate in deeper channels, where tidal currents are weak in and around seagrass leaves (Biber 2007) (Hawes and Smith 1995, Holmquist 1997, Cummins et al. 2004, Thomsen 2004, Huntington and Boyer 2008, Thomsen 2010, Halling et al. 2013). These drift algae accumulations support invertebrate communities because they build more complex habitat (Siciliano 2018), reduce abiotic desiccation stress (Lyons et al. 2014), is a food source for grazers, like many gastropods and amphipods (Jorgensen et al. 2010), and can reduce predation particularly on juvenile crabs (Johnston and Lipcius 2012, Thomsen et al. 2013). More specifically, habitat-users were more abundant when seagrasses and seaweeds co-occurred, supporting many other studies that have found positive effects of co-occurring habitat formers on invertebrate communities (Hooks et al. 1976, Gore et al. 1981, Pihl and Rosenberg 1982, Schneider and Mann 1991, Holmquist 1997, Thomsen et al. 2012a, Thomsen et al. 2013). Community structures were significantly affected by latitude, elevation and presences of both seagrass and seaweed, but with most data-variability explained by latitude, where *Zeacumantus* and polychaetes were more common in southern estuaries, and grazing snails in central estuaries (Fig 3.5.2.2) as also found by Foster (2019). Much of the large variation observed in community structures are likely explained by high variability in estuary types, areas and topography, catchment characteristics (Hume et al. 2007, Battley et al. 2011, Hume et al. 2016), ocean currents, nutrient flows and different thermal stress (Turner et al. 2007, Sanford and Kelly 2011, Vaquer-Sunyer and Duarte 2011).

3.4.3. Seasonal survey: quadrat data

Seasonal changes in cover types differed greatly between the Avon-Heathcote estuary and Duvauchelle Bay (Fig. 3.5.3.1.), with large variation in cover of seaweed, seagrass, and dead shells. Dead shells had higher cover at lower elevations, as was also found in the latitudinal survey. Differences between Duvauchelle Bay and the Avon-Heathcote Estuary may be because the latter is a bar built estuary with highly variable environmental conditions and seagrass only in the eastern parts), whereas the former is a smaller more uniform mudflat dominated by seagrass patches, particularly at lower elevations (Hume et al. 2007, Hume et al. 2016). Furthermore these estuaries have different entrances to the ocean (Roy et al. 2001) and sediment characteristics (Gray 2002, Bolton-Ritchie 2005, Thrush et al. 2006, Hume et

al. 2007, de Juan and Hewitt 2011, Bolton-Ritchie 2015) perhaps explaining why abundance and richness was higher in the Avon-Heathcote estuary throughout all seasons.

Seasonal fluctuations in the abundance of seaweeds and seagrass were observed in both estuaries. Seagrass decreased slightly at the end of summer but recovered throughout winter months, as found in other studies in New Zealand (Ismail 2002, Les et al. 2002, Robertson et al. 2002, Inglis 2003, Turner and Schwarz 2006, Turner 2007). By contrast, seaweed cover was more variable across seasons perhaps because seaweed respond more rapidly to changes in nutrient concentrations, riverine influx, temperature, and hydrodynamic conditions (Raffaelli et al. 1998, Thomsen and McGlathery 2007, Marsden and Knox 2008, Abreu et al. 2011, Zhang et al. 2016). Across all the sample locations in the Avon-Heathcote estuary dead shells were more abundant than seagrass (but less than mud and seaweed). Dead shells, dominated by bivalves, increases habitat heterogeneity in sedimentary systems (Jones et al. 1994, Gutiérrez et al. 2003, Sousa et al. 2009), and create 'satellite-habitats' that enhance local biodiversity (Posey et al. 1999, Lehnert and Allen 2002, Gutiérrez et al. 2003, Tolley and Volety 2005, Grabowski and Peterson 2007, Schejter and Bremec 2007, Gribben et al. 2009, Brett et al. 2011, Thomsen et al. 2016, Foster 2019). Again, these results highlight that these understudied habitats should be included in future surveys of estuarine biodiversity. By comparison, most estuarine biodiversity studies focus on bare sediments, seagrass and/or seaweeds (Raffaelli et al. 1998, Thomsen and McGlathery 2007, Marsden and Knox 2008, Abreu et al. 2011, Zhang et al. 2016). Still, a growing number of studies around the world have highlighted ecological legacy effects from dead shells (Posey et al. 1999, Lehnert and Allen 2002, Gutiérrez et al. 2003, Tolley and Volety 2005, Grabowski and Peterson 2007, Schejter and Bremec 2007, Gribben et al. 2009, Brett et al. 2011, Thomsen et al. 2016, Foster 2019).

In the Avon-Heathcote estuary, there were more habitat-interactions and higher habitat-interaction richness at the lower elevation (Fig. 3.5.3.4.) – a pattern that was consistent across months. This pattern is probably explained by lower desiccation stress and more foraging time at lower elevations (Grant and McDonald 1979, Omori et al. 1998, Bertness et al. 2001). However, this pattern was not observed in Duvauchelle Bay (Fig. 3.5.5.1B) possibly because the number of interactions was much smaller and elevation effects may have been random due to the smaller population sizes.

The organisms that explained most of the multivariate variability in habitat-interactions were all molluscs – i.e., mudsnails (*Amphibola crenata*), cockles (*Austrovenus stutchburyi*), and limpets (*Notoacmea helmsii*) (Fig. 3.5.3.5). During summer months, physiological stress can be high on these molluscs (Vaquer-Sunyer and Duarte 2011, Altieri and Gedan 2015, Cheng et al. 2015), and high-temperature and desiccation stress can lead to physiological changes in animals (Pörtner and Knust 2007, Rosenzweig et al. 2008, Delorme et al. 2020), seagrass (Turner et al. 2007, Short et al. 2014), and seaweeds (Vaquer-Sunyer and Duarte 2011). Mobile organisms can move between cover types to decrease these physiological stressors (Micheli and Peterson 1999, Wright et al. 2014). Mobility allows these organisms to move towards less stressful microhabitats, whereas other physiological adaptations, like burrowing into sediments or the closing of opercula (Foster 1971, Shumway and Marsden 1982, Lowell 1984) help to alleviate desecration stress within a microhabitat. I found that assessing the effect of dead shells, seaweeds, and seagrass on habitat-interactions gives more profound insight into the effects of season on estuarine communities.

3.4.4. Seasonal survey: core data

Richness and abundances of invertebrate habitat-users were generally low in bare sediments, high in summer at high elevation in the separate seagrass and seaweeds habitats, and high in winter at lower elevation when seagrass and seaweed co-occurred (Fig. 3.5.4.1., Tab.3.6.4). The morphology, structure, abundance and function can change across seasons for both temperate estuarine seagrass (Turner 1996, van Houte-Howes et al. 2004, Turner and Schwarz 2006, Turner et al. 2007, Battley et al. 2011) and seaweeds (Raffaelli et al. 1998, Thomsen and McGlathery 2007, Marsden and Knox 2008, Lyons et al. 2014, Zhang et al. 2016). These changes to habitat-formers are likely to have flow-on effects on the distribution and abundance of invertebrates between seasons.

Seagrass facilitates epifaunal habitat-users through their above-ground leaf structure (Heck Jr and Orth 1980, Bell et al. 2001, Turner and Schwarz , Duarte et al. 2007, Short et al. 2007), whereas infauna can be directly affected by below-ground rhizomes and root networks that also aid in stabilizing sediment (Bertness et al. 2001, Reise 2002, Newell and Koch 2004), which increases the recruitment of gastropods and bivalves (Bologna and Heck 2000, Boström and Bonsdorff 2000, Connolly and Hindell 2006). By comparison, seaweeds, are typically more variable across seasons and generally provide less habitat in winter (Norkko et al. 2000, Thomsen et al. 2013, Wright et al. 2014, Thomsen et al. 2016) (see also section

3.4.2.). Although seagrasses often have seasonal diebacks (Turner 1996, van Houte-Howes et al. 2004, Turner and Schwarz 2006, Turner et al. 2007) clonal perennial seagrass still provides a more stable habitat (in both space and time) to invertebrates than estuarine seaweeds that can break off from their substrates, drift around with currents, and die back dramatically over winter (Hawes and Smith 1995, Norkko et al. 2000, Thomsen 2004, Thomsen and McGlathery 2007, Marsden and Bressington 2009, Marsden and Maclaren 2010a, Thomsen et al. 2013, Wright et al. 2014, Thomsen et al. 2016).

Community structure was greatly affected by season and the presence of seagrass and seaweeds. As in latitudinal study, habitat-users were generally abundant and taxonomic rich when seagrasses and seaweeds cooccurred (Fig. 3.5.4.1.), thereby supporting many other similar 'facilitation cascade' studies (Hooks et al. 1976, Gore et al. 1981, Pihl and Rosenberg 1982, Schneider and Mann 1991, Holmquist 1997, Thomsen et al. 2012a, Thomsen et al. 2013, Thomsen et al. 2018b, Gribben et al. 2019). Seasonal variation in invertebrate community structure is often explained by a combination of seasonal variation in abundance of the habitat formers themselves (Turner , Norkko et al. 2000, van Houte-Howes et al. 2004, Turner and Schwarz 2006, Turner et al. 2007, Thomsen et al. 2013, Wright et al. 2014, Thomsen et al. 2016) as well as habitat preferences by habitat-users (Holmquist 1997, Cummins et al. 2004). More specifically, much of the data variability (Fig.3.5.4.2.) observed here was attributed to the highly abundant grazing snail, *Micrelenchus tenebrosus* that was more common in winter, and partly also to bivalves and polychaetes that were most abundant in summer as also shown in other studies from this region (Thomsen et al. 2016, Siciliano 2018, Foster 2019, Siciliano et al. 2019) and from seagrass beds on the North Island (Duncan 2017). Studies from other seagrass beds around the world have also found more invertebrates in summer months (Edgar 1990, Nelson and Waaland 1997, Bloomfield and Gillanders 2005).

3.5.5. Data limitations

The collected data had limitations that can affect analyses and interpretations. For example, the latitudinal quadrat survey was unbalanced because only eight out of twelve quadrats were sampled in Okiwa Bay because of time constrains and poor weather. However, factorial MANOVA is relatively robust to a slightly unbalanced design (Scheiner 1993, Shaw and Mitchell-Olds 1993, Berger et al. 1999, Gastwirth et al. 2009). In the seasonal quadrat survey, relatively few taxa were common, so species rarefication curves could have been added to

better understand which species were over or underrepresented (Heck et al. 1975). I did find significant effects of season and cover types on invertebrate core communities, probably because time-constrains limited my field sampling and sample processing to only two replicates at the lowest sampling level (i.e., for each combination of elevation, location, seasons and presence of seaweed and seagrass). Future core-studies should include sampling across more months as well as more replicates on the lowest levels to understand temporal variability in estuarine invertebrate community structures (Chesson 1985, Wolfe et al. 1987, Triantis et al. 2003, Lindenmayer and Likens 2009, Shen et al. 2009, Magurran et al. 2010, Scheiner et al. 2011, White et al. 2018). Finally, future studies should also collect detailed abiotic data to explore relationships with the biotic data, for example by measuring current velocities, turbidity (Lenihan et al. 2001, Lunt and Smee 2014), nutrient levels, sediment properties, and air and sea surface temperature (Dijkstra et al. 2012, Cheng et al. 2015, Thomson et al. 2015, Lauchlan and Nagelkerken 2020), estuary size, depth and morphology, as well as large-scale catchment properties.

3.5.6. Conclusion

This study found consistent, strong effects of elevation on invertebrates in cores and interactions between habitat-formers and habitat-users – with higher diversity and more interactions at lower elevations (Siciliano 2018, Foster 2019). In addition there was strong community effects between latitudes, highlighting that community analysis is more sensitive to detect larger-scale biogeographical patterns than abundances and richness metrics (Clarke and Gorley 2015). Importantly, dead shells on sediment surfaces were found to provide habitat for many species across latitudes, elevations, and seasons. Dead shells are often overlooked as important habitats in estuarine biodiversity surveys. The species that explained most variation in the latitudinal survey were gastropods (*Diloma* spp., *Micrelenchus tenebrosus*), limpets (*Notoacmea*), bivalves (*Austrovenus stutchburyi*), and seaweeds (*Ulva* and *Agarophyton chilensis).* In the seasonal survey, mollusc like *M. tenebrosus, Notoacmea,* and *A. stutchburyi* explained most of the variation in multivariate community structure and more habitat-users were found at low elevations in winter, possible because invertebrates 'concentrate' around estuarine foundation species that are less common in this season (seaweed in particular). The data collected here provide important baseline information about estuarine habitat-users across a range of latitudes, elevation, and seasons to gauge future impacts of climate changes and other human stressors.

3.5. Figures

Figure 3.5.1. Latitudinal survey: Quadrats

Figure 3.5.1.1. Latitudinal survey: Quadrats – cover types of habitat formers

Percent cover of the most common habitat types found in the latitudinal survey quadrats at two elevations (high, low) and three regions (north = N, central = C, south = S). Quadrat size = 0.010 m^2.

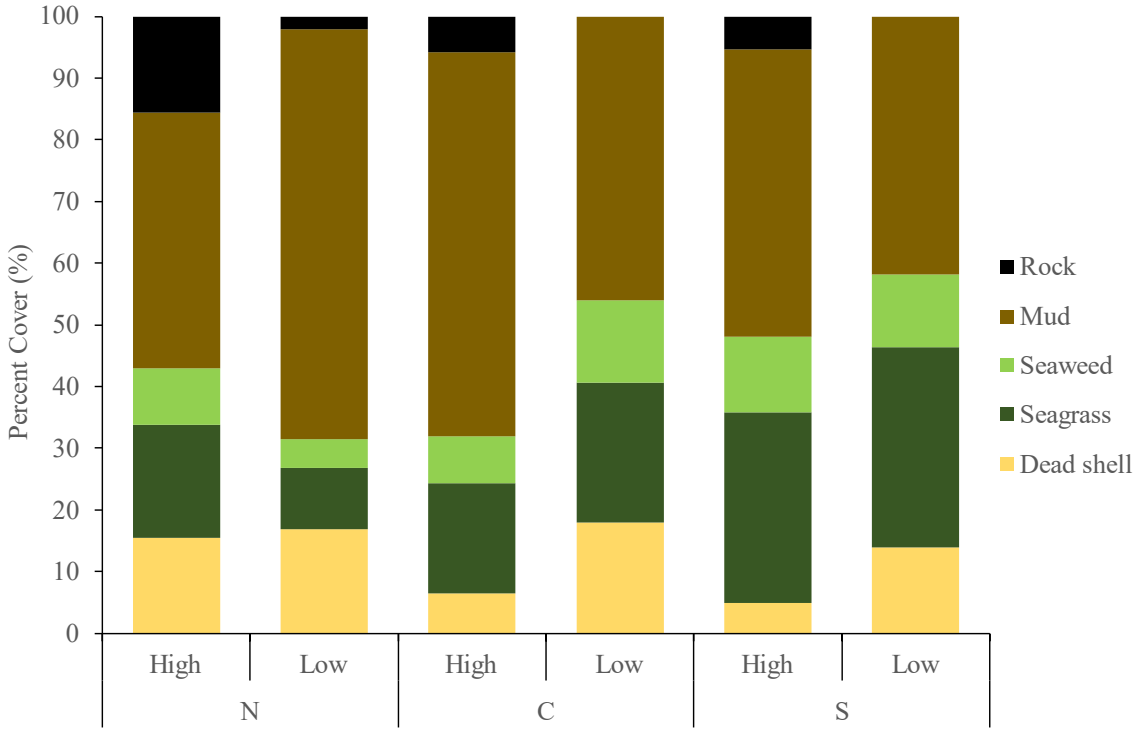


Figure 3.5.1.2. Latitudinal survey: Quadrats – 'abundance' and 'richness' of habitat-interactions

The mean number of interactions (A) and interaction-richness (B) (+SE) per quadrat across northern, central, and southern regions (pooled across estuarine impact levels per region). Quadrat size = 0.010m^2.

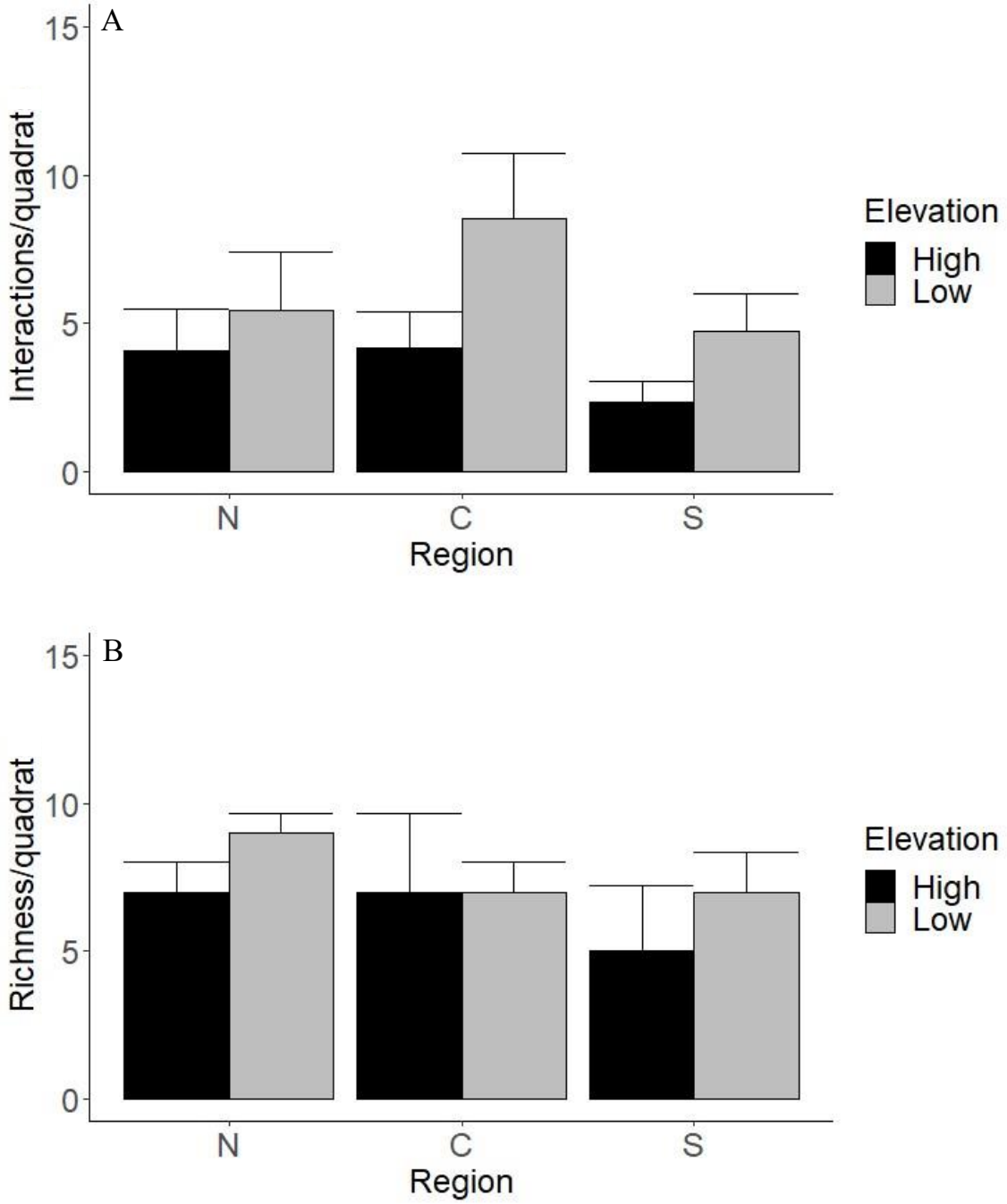


Figure 3.5.1.3. Latitudinal survey: Quadrats – 'community pattern' of habitat-interactions

Principle coordinate analysis for latitudinal quadrat communities. Legend: First letter = region (N = North, C = Central, S = South), second letter = elevation (H = high, L = Low), third letter = habitat (blank = Bare, G = seagrass, W = seaweed, GW = seagrass and seaweed). Colour coding: North high = Black, low = grey; Central high = dark blue, low = light blue solid fill, and South high = dark green, low = light green. Symbols: Solid = high and open = low elevation. Overlay vectors are abbreviated by numbers representing habitat-user followed by habitat former: 1: *Ulva*-Dead shell, 2: *Notoacmea helmsi-Diloma* spp., 3: *Austrovenus stutchburyi-Zostera muelleri*, 4: *Diloma* spp.-Dead shell, 5: *Gigartina spp.-Micrelenchus tenebrosus*, 6: *Notoacmea helmsi*-Dead shell, 7: *Micrelenchus tenebrosus*-Dead shell, 8: *Anthopleura aureoradiata-Austrovenus stutchburyi*, 9: *Notoacmea helmsi-Austrovenus stutchburyi*, 10: *Austrovenus stutchburyi*,-Mud, 11: *Agarophyton chilensis-Austrovenus stutchburyi*. Bray-Curtis similarity matrix of square root transformed community data with a dummy variable of one (n = 1) was used. Pearson correlation set to > 0.25.

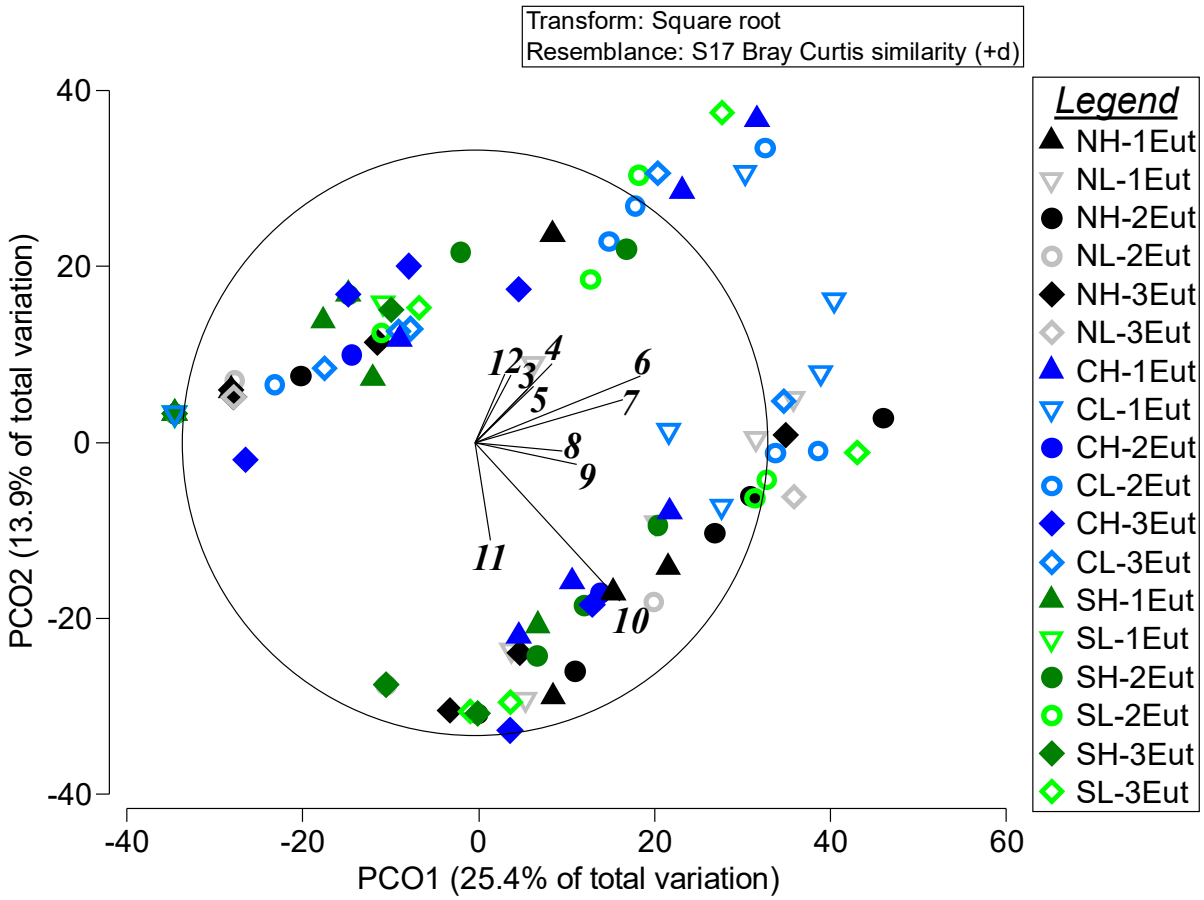


Figure 3.5.2. Latitudinal survey: Cores

Figure 3.5.2.1. Latitudinal survey: Cores - abundances and richness of habitat-users

Latitudinal survey of habitat-users in sediment cores across latitudes. Mean abundance (A) and richness (B) of invertebrates per core (+ SE) at high and low elevations across northern, central, and southern regions in the absence and presence of the seagrass *Zostera muelleri* (SG) and the seaweed *Ulva* spp. (SW). Estuaries within each region were pooled. Bare = mud (i.e., cores without any habitat-forming foundation species). Cores were 0.0064 m^2.

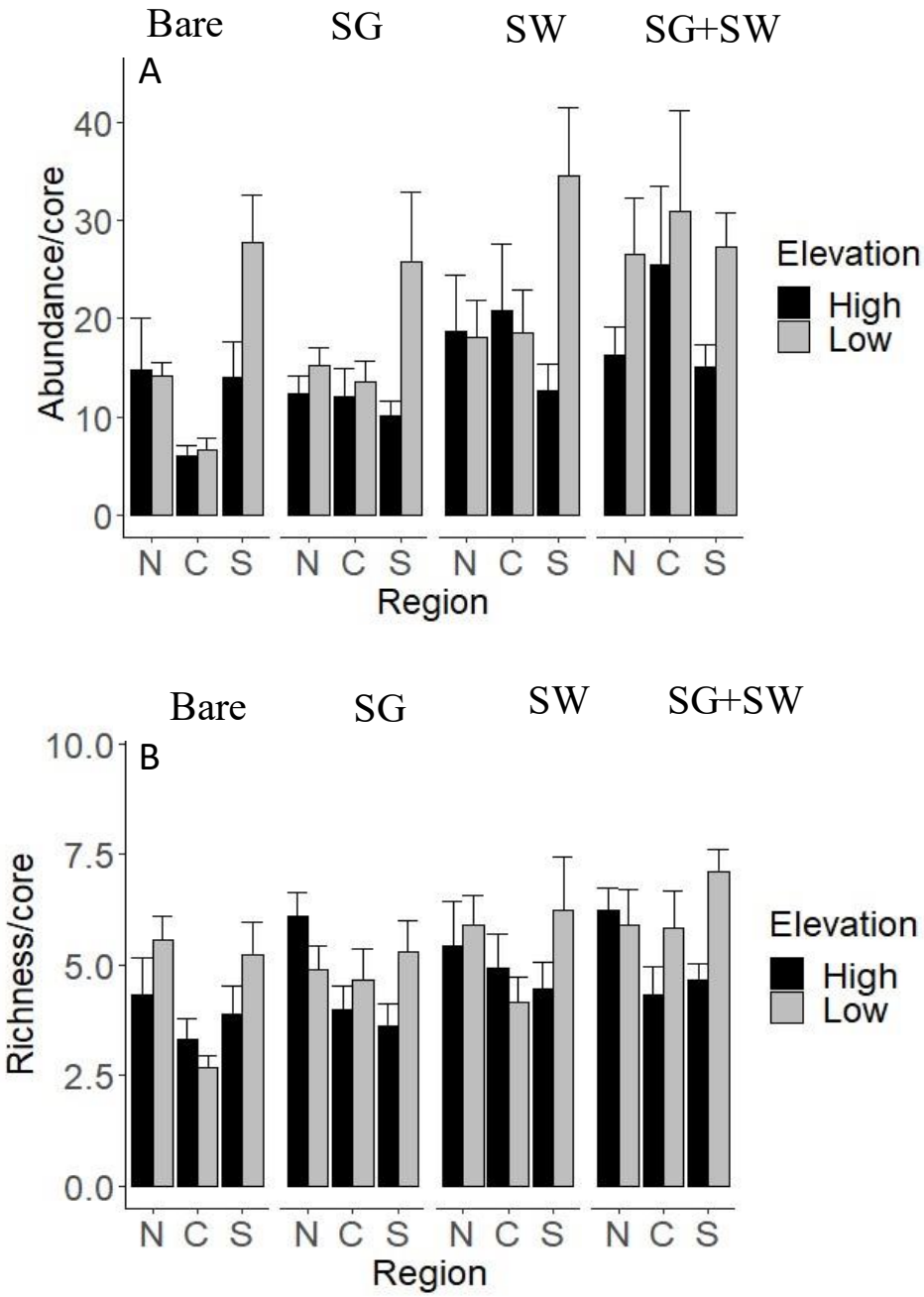


Figure 3.5.2.2. Latitudinal survey: Cores – community pattern of habitat-users
Principle coordinate analysis for seasonal core communities. The first letter is region (N = North, C = Central, S = South), followed by elevation (H = high, L = Low), then core type (blank = Bare, G = seagrass, W = seaweed, GW = seagrass and seaweed). Regional elevation change is broken down into colour and fill categorization with North high = Black, low = grey; Central high = dark blue, low = light blue solid fill, and South high = dark green, low = light green. Solid symbols represent high elevation with open symbols representing low elevation. Overlay vectors are abbreviated by number representing species: 1: Errantia, 2: *Anthopleura aureoradiata*, 3: *Edwardsia leucomelos*, 4: Amphipoda spp., 5: *Diloma subrostrata*, 6: *Halicarcinus whitei*, 7: Isopoda spp., 8: *Macomona liliana*, 9: *Micrelenchus tenebrosus*, 10: *Notoacmea helmsi*, 11: Sedentaria, 12: *Zeacumantus subcarinatus*. Bray-Curtis similarity matrix of square root transformed community data with a dummy variable of one (n = 1) was used. Pearson correlation set to > 0.25.

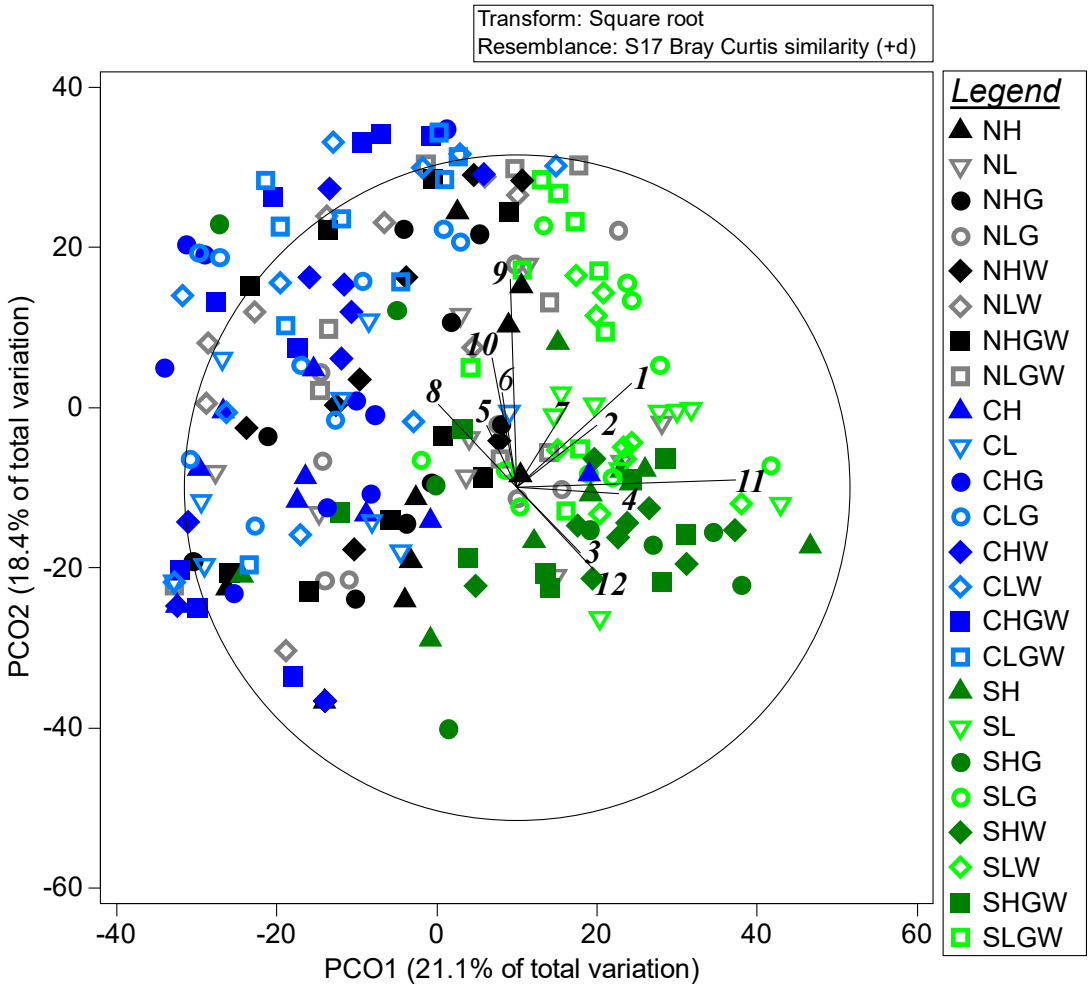


Figure 3.5.3. Seasonal survey: Quadrats

Figure 3.5.3.1. Seasonal survey: Quadrats - cover types of habitat formers

Percent cover of the most common types of habitats found in seasonal quadrat survey in 2020 in the Avon-Heathcote estuary (A) and Duvauchelle Bay (B). Locations within an estuary were pooled. Sampling started one month earlier in the Avon-Heathcote estuary. Quadrat size = 0.0625 m^2.

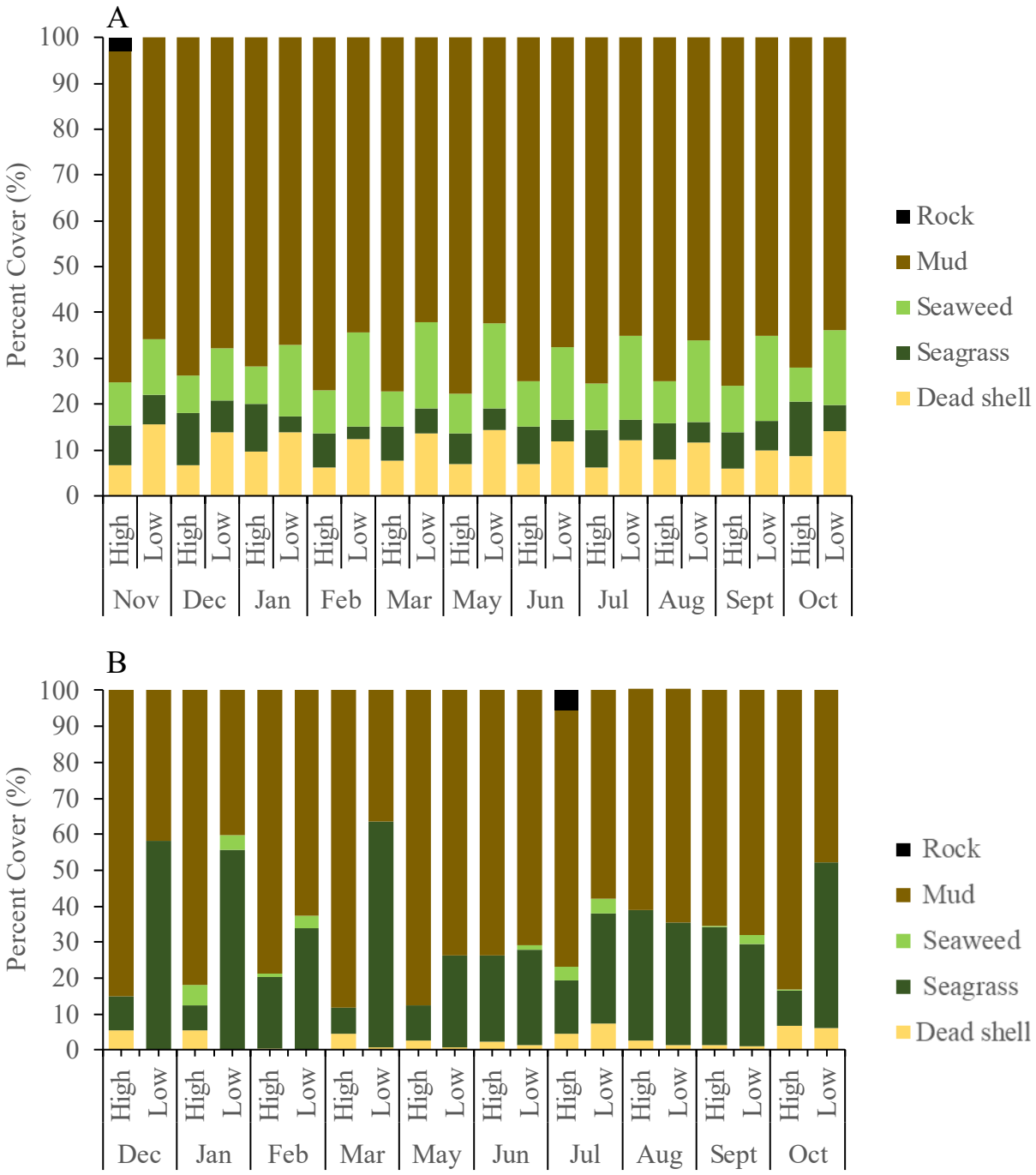


Figure 3.5.3.2. Seasonal survey: Quadrats - 'abundance' of habitat-interactions per month

Mean number of habitat-interactions per quadrat (+SE) per month in Avon-Heathcote estuary (A) and Duvauchelle bay (B) at high and low elevations. Locations within each estuary were pooled. Quadrat size = 0.0625 m^2.

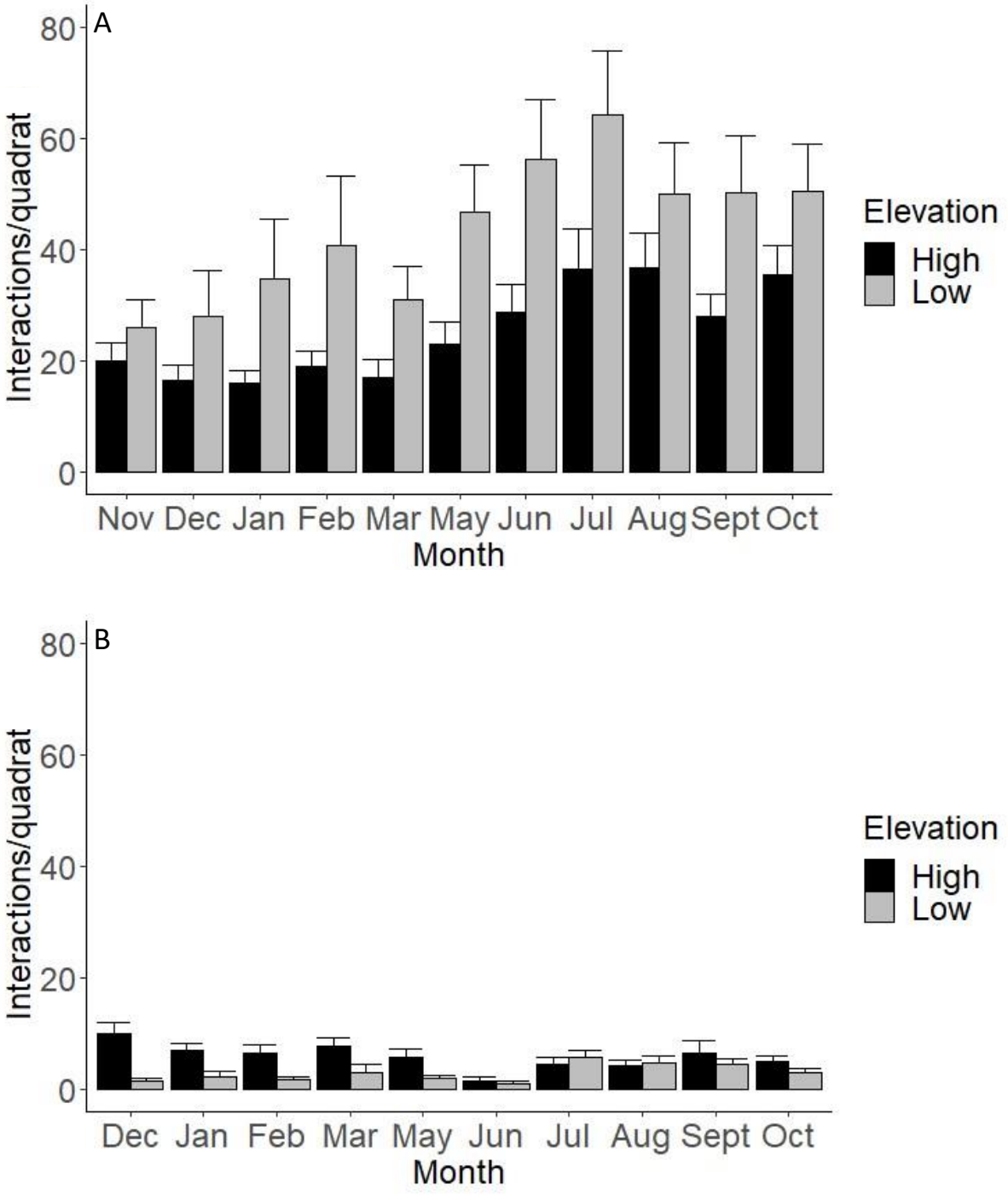


Figure 3.5.3.3. Seasonal survey: Quadrats – 'richness' of habitat-interactions per month
Mean richness of habitat-interactions per quadrat (+SE) per month in Avon-Heathcote estuary (A) and Duvauchelle bay (B) at high and low elevations. Locations within each estuary were pooled. Quadrat size = 0.0625 m^2.

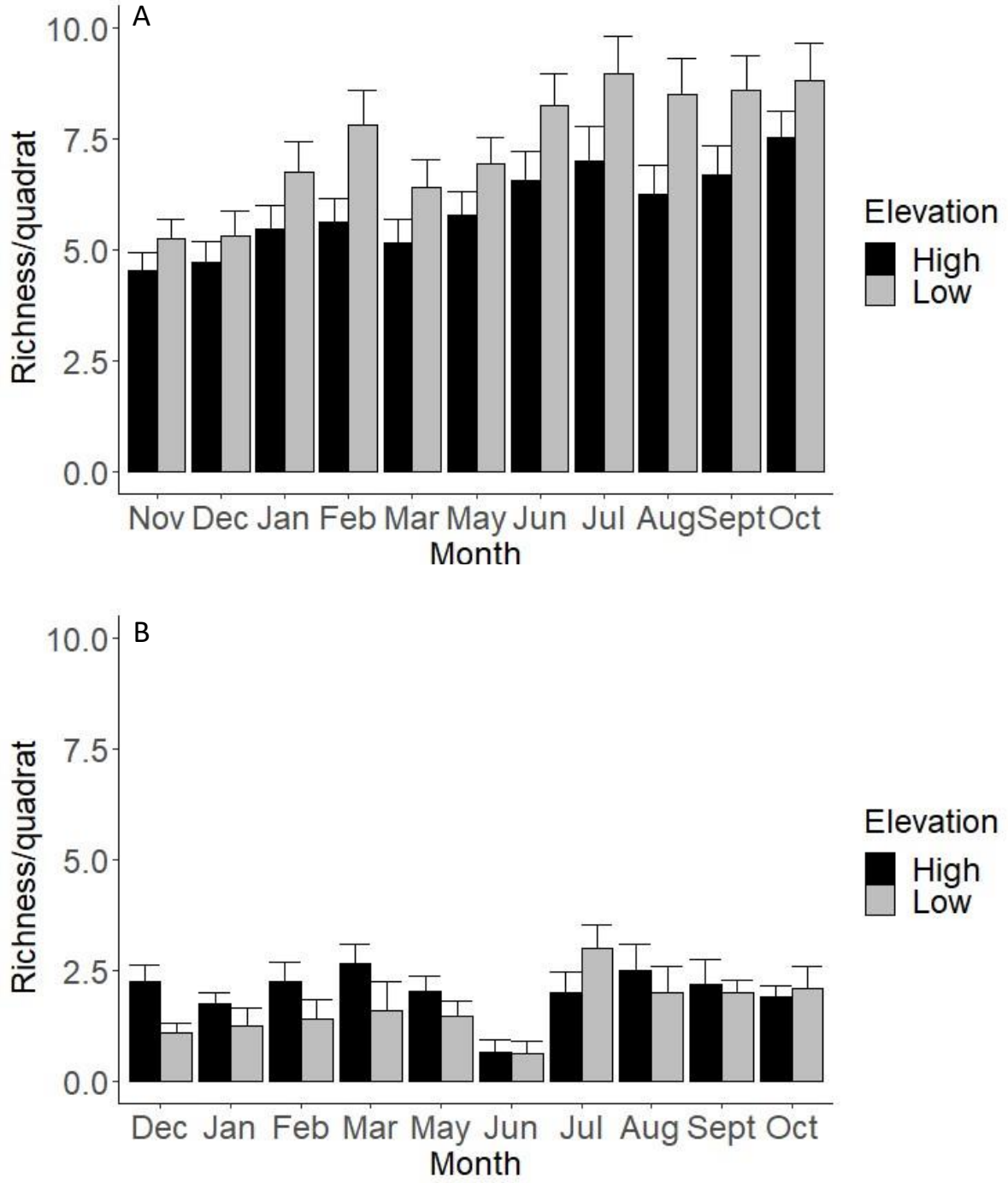


Figure 3.5.3.4. Seasonal survey: Quadrats - 'abundance' and 'richness' of habitat-interactions per season

The mean number of interactions (A) and interaction-richness (B) (+SE) per quadrat contrasted between warmer summer vs. colder winter seasons in the Avon Heathcote Estuary (AHE) and Duvauchelle Bay (DUV) at high and low elevation. Quadrat size = 0.0625 m^2.

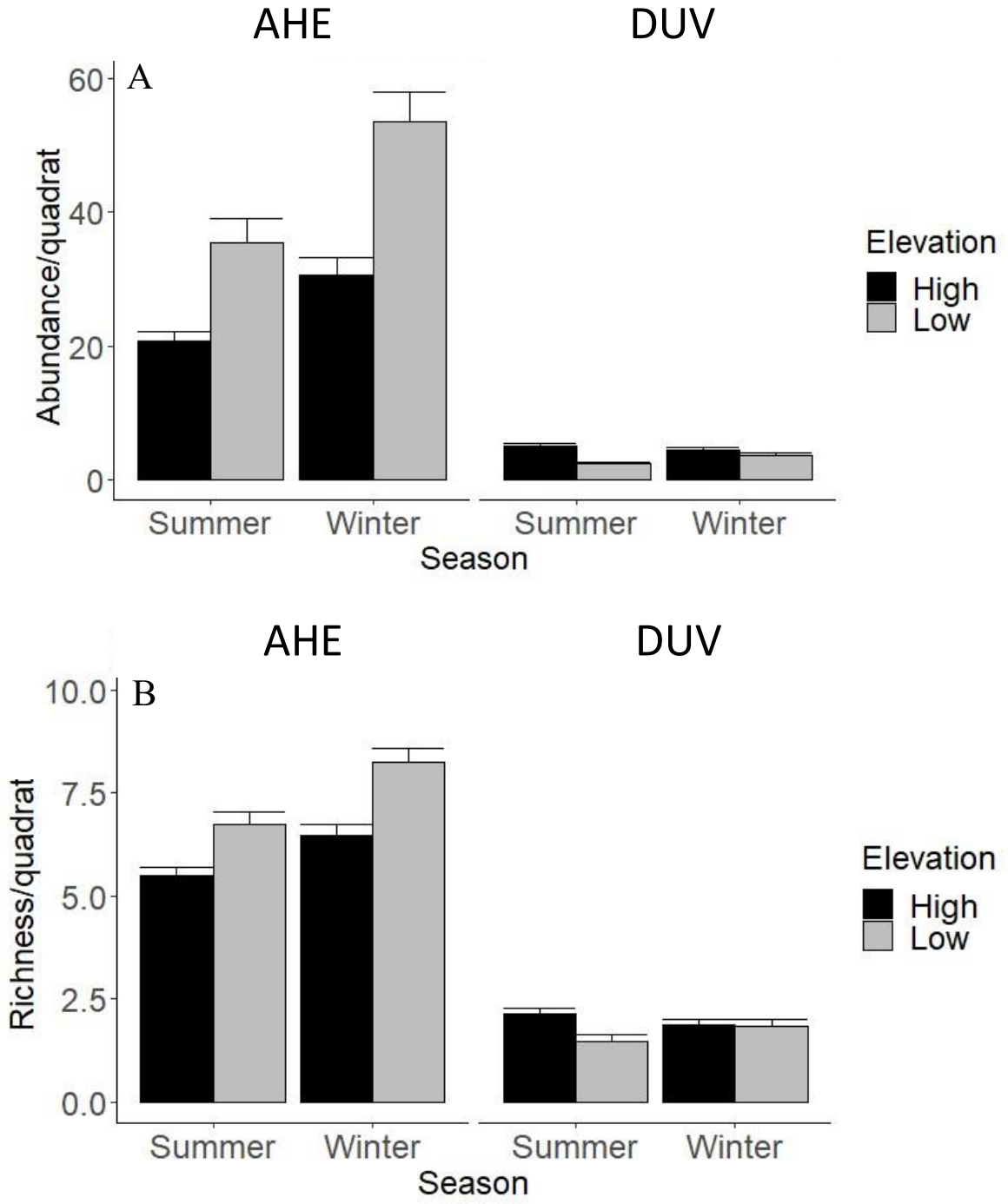


Figure 3.5.3.5. Seasonal survey: Quadrats – 'community pattern' of habitat-interactions
Principle coordinate analysis for seasonal quadrat communities. The first letter in the legend represents season (S =summer, W= winter), followed by elevation (H = high, L = Low) and estuary (AHE = Avon Heathcote and DUV=Duvauchelle Bay). Bray-Curtis similarity matrix of square root transformed community data with a dummy variable of one was used. Pearson correlation coefficient was set to > 0.20 and overlay vectors numbers represents habitat-user-on-habitat-former: 1: *Amphibola crenata*-Mud, 2: *Austrovenus stutchburyi*-Mud, *3: Ulva-Austrovenus stutchburyi*, *4: Diloma*-Mud, *5: Ulva-Diloma, 6: Cominella glandiformis*-Mud , *7: Micrelenchus tenebrosus -Ulva, 8: Ulva*-Dead shell, *9: Diloma*-Dead shell, *10: Notoacmea helmsi*-Dead shell, *11: Notoacmea helmsi-Diloma, 12: Micrelenchus tenebrosus*-Dead shell, *13: Elminius modestus*-Dead shell, *14 : Micrelenchus tenebrosus-Zostera muelleri.*

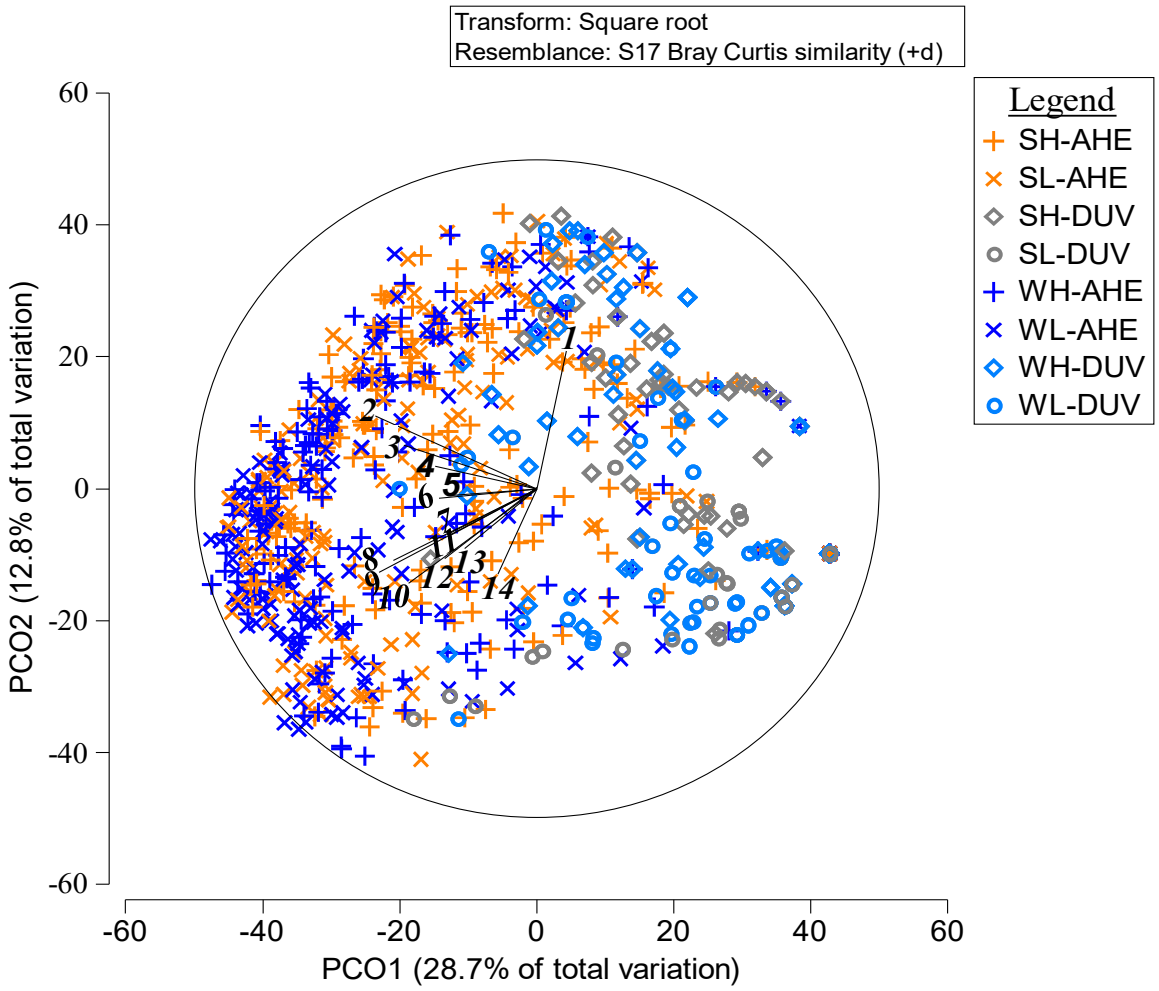


Figure 3.5.4. Seasonal survey: cores

Figure 3.5.4.1. Seasonal survey: Cores - abundance and richness of habitat-users

Mean abundance m^{-2}+ SE (A) and richness m^{-2} + SE (B) of invertebrates in the Avon Heathcote estuary in high (black) and low (grey) elevations in summer (S) and winter (W) in the absence and presence of the seagrass *Zostera muelleri* (SG) and seaweed *Ulva* spp. (SW). Locations within each estuary were pooled. Bare = mud cores without any habitat-forming foundation species. Sampling cores were 0.0064 m^2

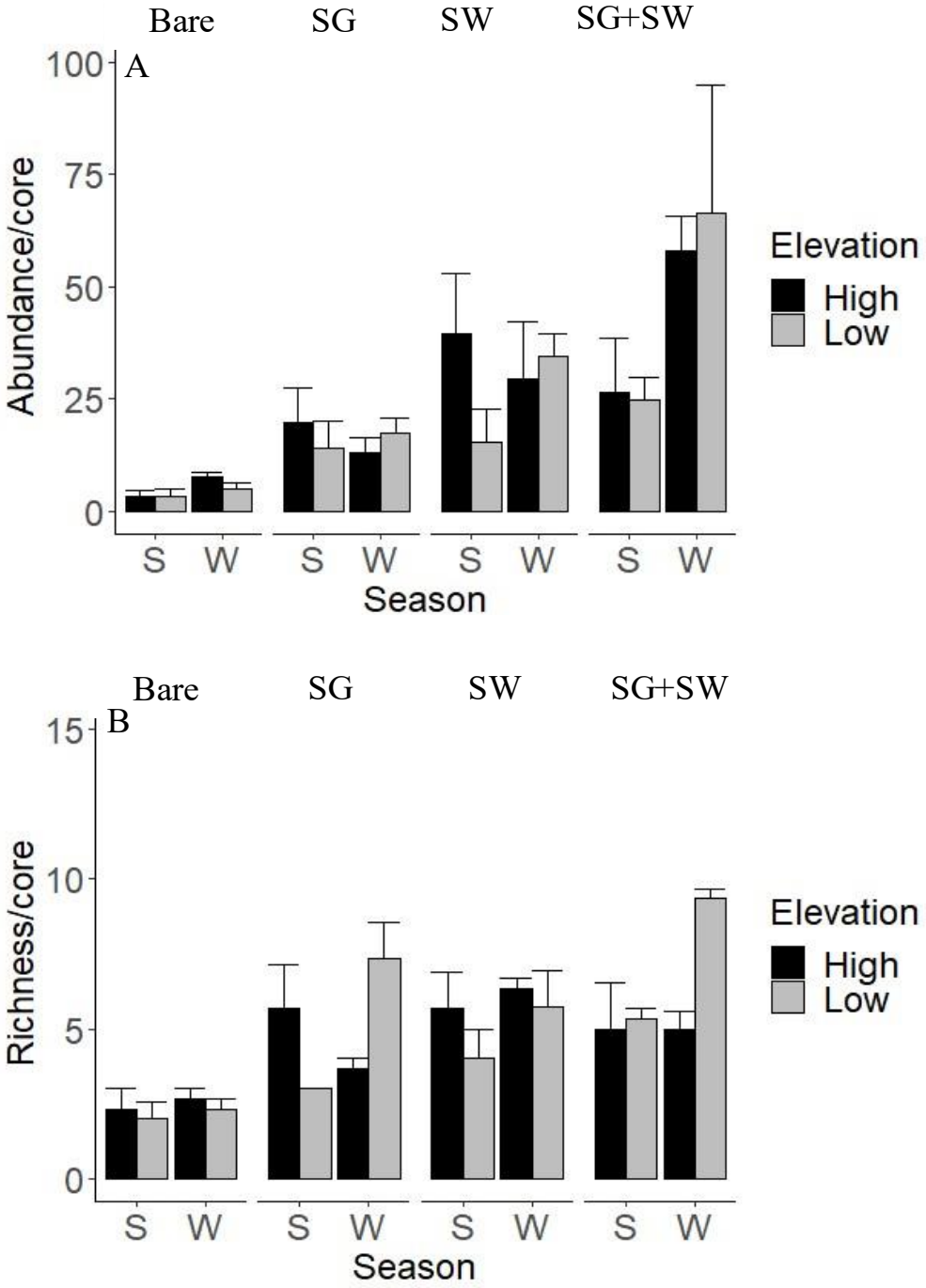
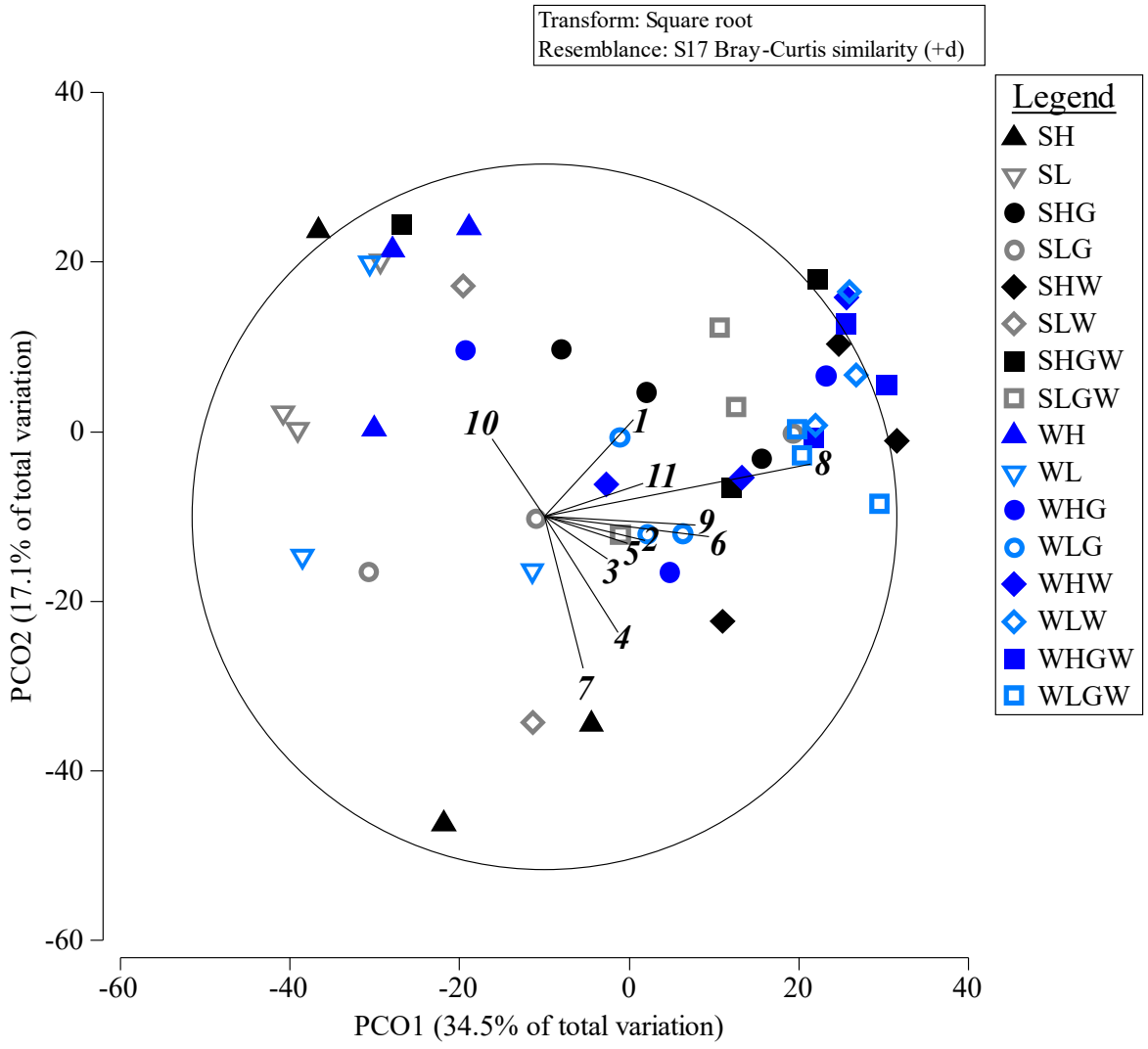


Figure 3.5.4.2. Seasonal survey: Cores - community pattern of habitat-users
Principle coordinate analysis for seasonal core communities. The first letter in the legend represent season (S =summer, W= winter), follow by elevation (H = high, L = Low) and habitat type (blank = bare, G = seagrass, W = seaweed, GW = co-occurring seagrass and seaweed). Color-coding: summer high = Black, low = grey; Winter high = dark blue, low = light blue solid fill. Solid symbols represent high elevation with open symbols representing low elevation. Bray-Curtis similarity matrix of square root transformed community data with a dummy variable of one was used. The correlation coefficient was set to >0.20 and the overlay vectors are abbreviated by numbers representing invertebrates in cores; 1: Errantia, 2: *Macrophthalmus hirtipes*, 3: *Diloma subrostrata*, 4: *Diloma nigerrima*, 5: *Dosinia anus*, 6: *Halicarcinus whitei*, 7: *Macomona liliana*, 8: *Micrelenchus tenebrosus*, 9: *Notoacmea helmsi*, 10: *Paphies australis*, 11: Sedentaria.



3.6. Tables

Table 3.6.1. Latitudinal survey: Quadrats

Three-way permutational (M)ANOVA testing for effects of latitudinal region (north, central, south), elevation (high, low), and anthropogenic stress (low, moderate, high) on abundances (A), richness (B) and community structure (C) of unique habitat-interactions. Significant P-values ($p < 0.05$) are in bold.

Response	Test Factors	Df	SS	F	P
(A) Abundance	Region	2	18.010	2.248	0.1118
	Elevation	**1**	**8.916**	**5.381**	**0.0227**
	Stress	2	1.617	2.578	0.0818
	Region x Elevation	2	11.820	1.116	0.3322
	Region x Stress	**4**	**121.563**	**5.022**	**<0.001**
	Elevation x Stress	2	9.170	1.986	0.1434
	Region x Elevation x Stress	**4**	**46.825**	**2.832**	**0.0294**
	Res	86	336.333		
(B) Richness	Region	2	18.010	2.303	0.1061
	Elevation	1	8.916	2.280	0.1347
	Stress	2	1.617	0.207	0.8136
	Region x Elevation	2	11.820	1.511	0.2265
	Region x Stress	**4**	**121.563**	**7.771**	**<0.001**
	Elevation x Stress	2	9.170	1.172	0.3145
	Region x Elevation x Stress	**4**	**46.825**	**2.993**	**0.0230**
	Residuals	86	336.333		
(C) Community	**Region**	**2**	**11074**	**2.797**	**<0.001**
	Elevation	1	2967.8	1.499	0.135
	Stress	2	5819.9	1.470	0.081
	Region x Elevation	**2**	**6408.7**	**1.618**	**0.038**
	Region x Stress	**4**	**20698**	**2.613**	**<0.001**
	Elevation x Stress	2	3123.9	0.789	0.7464
	Region x Elevation x Stress	**4**	**15685**	**1.980**	**<0.001**
	Residuals	86	1.70E+05		

Table 3.6.2. Latitudinal survey: Cores

Four-way permutational (M)ANOVA testing for the effects of latitudinal region (north, central, south), elevation (high, low), presence/absence of seagrass, and presence/absence of seaweed on abundance (A), richness (B) and multivariate community structure (C) of invertebrates. Levine's homogeneity test of variance was significant for community analysis which were therefore square root transformed. Euclidean distance was used in the resemblance matrix for richness and abundance and Bray-Curtis for community structure. Permutations were set to n = 4999. Estuaries within each region were pooled. Significant P-values are in bold.

Response	Test Factors	Df	SS	F	P
(A) Abundance	Seagrass	1	277.46	1.296	0.256
	Seaweed	**1**	**2998.9**	**14.003**	**<0.001**
	Elevation	**1**	**3230.1**	**15.082**	**<0.001**
	Latitude	2	918.31	2.144	0.125
	Seagrass x Seaweed	1	236.73	1.105	0.304
	Seagrass x Elevation	1	62.68	0.293	0.594
	Seagrass x Latitude	2	1116.1	2.606	0.071
	Seaweed x Elevation	1	150.18	0.701	0.417
	Seaweed x Latitude	2	1086	2.535	0.074
	Elevation x Latitude	**2**	**1815.3**	**4.238**	**0.012**
	Seagrass x Seaweed x Elevation	1	6.6973	0.031	0.853
	Seagrass x Seaweed x Latitude	2	134.9	0.315	0.741
	Seagrass x Elevation x Latitude	2	279.42	0.652	0.540
	Seaweed x Elevation x Latitude	2	7.0151	0.016	0.983
	Seagrass x Seaweed x Elevation x Latitude	2	203.93	0.476	0.626
	Residuals	193	41333		
(B) Richness	Seagrass	1	14.318	3.421	0.063
	Seaweed	**1**	**43.225**	**10.327**	**0.001**
	Elevation	**1**	**35.862**	**8.568**	**0.005**
	Latitude	**2**	**59.287**	**7.083**	**0.001**
	Seagrass x Seaweed	1	0.004	0.001	0.976
	Seagrass x Elevation	1	2.737	0.654	0.424
	Seagrass x Latitude	2	3.390	0.405	0.674
	Seaweed x Elevation	1	1.148	0.274	0.616
	Seaweed x Latitude	2	1.985	0.237	0.792
	Elevation x Latitude	**2**	**29.635**	**3.540**	**0.036**
	Seagrass x Seaweed x Elevation	1	1.208	0.289	0.585
	Seagrass x Seaweed x Latitude	2	2.865	0.342	0.707
	Seagrass x Elevation x Latitude	**2**	**37.458**	**4.475**	**0.015**
	Seaweed x Elevation x Latitude	2	0.726	0.087	0.919
	Seagrass x Seaweed x Elevation x Latitude	2	2.094	0.250	0.784
	Residuals	193	807.800		
(A) Community	**Seagrass**	**1**	**5015.400**	**3.517**	**0.002**

Seaweed	**1**	**7386.100**	**5.179**	**<0.001**
Elevation	**1**	**13530.000**	**9.487**	**<0.001**
Latitude	**2**	**54114.000**	**18.972**	**<0.001**
Seagrass x Seaweed	1	556.470	0.390	0.902
Seagrass x Elevation	1	1192.200	0.836	0.583
Seagrass x Latitude	2	3395.400	1.190	0.280
Seaweed x Elevation	1	1823.700	1.279	0.270
Seaweed x Latitude	2	3685.600	1.292	0.197
Elevation x Latitude	**2**	**6084.200**	**2.133**	**0.008**
Seagrass x Seaweed x Elevation	1	780.280	0.547	0.801
Seagrass x Seaweed x Latitude	2	2144.900	0.752	0.735
Seagrass x Elevation x Latitude	2	3632.300	1.273	0.219
Seaweed x Elevation x Latitude	2	2659.100	0.932	0.531
Seagrass x Seaweed x Elevation x Latitude	2	2286.4	0.8016	0.681
Residuals	193	2.75E+05		

Table 3.6.3. Seasonal survey: Quadrats

Three-way permutational (M)ANOVA testing effects of season (summer, winter), elevation (high, low), and estuary (Avon Heathcote, Duvauchelle Bay) on abundances (A), richness (B) and community structure (C) of unique habitat-interactions. Euclidean distance was used in the resemblance matrix for richness and abundance and Bray-Curtis for community structure. Permutations were set to 4999. Locations within estuaries were pooled. Significant P-values ($p < 0.05$) are in bold.

Response	Test Factors	Df	SS	F	P
(A) Abundance	**Season**	**1**	**17892.159**	**18.787**	**<0.001**
	Elevation	**1**	**27354.791**	**28.722**	**<0.001**
	Estuary	**1**	**263700.318**	**276.884**	**<0.001**
	Season x Elevation	**1**	3078.199	3.232	0.0725
	Season x Estuary	**1**	**15509.876**	**16.285**	**<0.001**
	Elevation x Estuary	**1**	**32933.687**	**34.580**	**<0.001**
	Season x Elevation x Estuary	**1**	255.514	0.268	0.6046
	Residuals	1156	1100959.186		
(B) Richness	**Season**	**1**	**158.623**	**17.738**	**<0.001**
	Elevation	**1**	**165.419**	**18.498**	**<0.001**
	Estuary	**1**	**6722.649**	**751.754**	**<0.001**
	Season x Elevation	**1**	24.849	2.779	0.0958
	Season x Estuary	**1**	**99.552**	**11.132**	**<0.001**
	Elevation x Estuary	**1**	**245.085**	**27.406**	**<0.001**
	Season x Elevation x Estuary	**1**	0.176	0.020	0.8885
	Residuals	1156	10337.664		
(C) Community	**Season**	**1**	**31339**	**14.162**	**<0.001**
	Elevation	**1**	**55604**	**25.127**	**<0.001**
	Estuary	**1**	**4.74E+05**	**214.08**	**<0.001**
	Season x Elevation	**1**	**17612**	**7.9591**	**<0.001**
	Season x Estuary	**1**	**12439**	**5.6213**	**<0.001**
	Elevation x Estuary	**1**	**53740**	**24.285**	**<0.001**
	Season x Elevation x Estuary	**1**	**12668**	**5.7247**	**<0.001**
	Residuals	1156	2.56E+06		

Table 3.6.4. Seasonal survey: Cores

Four-way permutational (M)ANOVA testing for the effects of season (summer, winter), elevation (high, low), presence/absence of seagrass, and presence/absence of seaweed on richness (A), abundance (B) and multivariate community structure (C) of invertebrates in the Avon Heathcote estuary. Levine's homogeneity test of variance was significant for the community analysis and data were square root transformed prior to analysis. Euclidean distance was used in the resemblance matrix for richness and abundance and Bray-Curtis for community structure. Permutations were set to 4999. Locations within the estuary were pooled. Significant P-values are in bold.

Response	Test Factors	Df	SS	F	P
(A) Abundance	**Seagrass**	**1**	**1873.100**	**6.315**	**0.014**
	Seaweed	**1**	**8056.400**	**27.159**	**<0.001**
	Elevation	1	55.682	0.188	0.680
	Season	**1**	**1288.000**	**4.342**	**0.038**
	Seagrass x Seaweed	1	26.914	0.091	0.776
	Seagrass x Elevation	1	144.250	0.486	0.500
	Seagrass x Season	1	566.790	1.911	0.176
	Seaweed x Elevation	1	16.409	0.055	0.833
	Seaweed x Season	1	1129.900	3.809	0.058
	Elevation x Season	1	376.410	1.269	0.283
	Seagrass x Seaweed x Elevation	1	118.230	0.399	0.552
	Seagrass x Seaweed x Season	1	1009.100	3.402	0.070
	Seagrass x Elevation x Season	1	5.500	0.019	0.898
	Seaweed x Elevation x Season	1	172.850	0.583	0.459
	Seagrass x Seaweed x Elevation x Season	1	172.850	0.583	0.461
	Residuals	31	9195.800		
(B) Richness	**Seagrass**	**1**	**33.960**	**16.622**	**0.001**
	Seaweed	**1**	**52.545**	**25.720**	**<0.001**
	Elevation	1	0.990	0.485	0.493
	Season	**1**	**14.727**	**7.209**	**0.016**
	Seagrass x Seaweed	**1**	**8.909**	**4.361**	**0.047**
	Seagrass x Elevation	**1**	**14.727**	**7.209**	**0.012**
	Seagrass x Season	1	2.444	1.197	0.283
	Seaweed x Elevation	1	0.505	0.247	0.623
	Seaweed x Season	1	1.636	0.801	0.381
	Elevation x Season	**1**	**22.000**	**10.768**	**0.002**
	Seagrass x Seaweed x Elevation	1	5.838	2.858	0.107
	Seagrass x Seaweed x Season	1	0.020	0.010	0.917
	Seagrass x Elevation x Season	**1**	**16.990**	**8.316**	**0.005**
	Seaweed x Elevation x Season	1	0.505	0.247	0.615
	Seagrass x Seaweed x Elevation x Latitude	1	1.636	0.801	0.374
	Residuals	31	63.333		
(A) Community	**Seagrass**	**1**	**3482.400**	**3.522**	**0.003**
	Seaweed	**1**	**8740.700**	**8.839**	**<0.001**

Elevation	1	1924.100	1.946	0.084
Season	**1**	**2522.800**	**2.551**	**0.024**
Seagrass x Seaweed	**1**	**3087.300**	**3.122**	**0.009**
Seagrass x Elevation	1	764.460	0.773	0.589
Seagrass x Season	**1**	**2388.500**	**2.415**	**0.033**
Seaweed x Elevation	1	1334.800	1.350	0.263
Seaweed x Season	1	1662.000	1.681	0.138
Elevation x Season	**1**	**2606.300**	**2.636**	**0.020**
Seagrass x Seaweed x Elevation	1	478.270	0.484	0.803
Seagrass x Seaweed x Season	1	1647.700	1.666	0.144
Seagrass x Elevation x Season	**1**	**3254.200**	**3.291**	**0.007**
Seaweed x Elevation x Season	1	1934.900	1.957	0.084
Seagrass x Seaweed x Elevation x Latitude	1	1352.300	1.368	0.237
Residuals	31	30654.000		

Chapter 4: General discussion

In this thesis, I quantified the distribution and abundances of estuarine foundation species (Chapter 2) and their associated communities (Chapter 3) across latitudinal and seasonal gradients. Analyses of distribution of foundation species were done based on drone images (landscape scales) and close-up digital photos (small scales) whereas effects on associated ecological communities were evaluated from core and quadrat data. Sites sampled in the seasonal and latitudinal surveys were selected based on previous work done at the same sites (Siciliano 2018, Foster 2019) using similar methodologies to enable detections of future long-term changes and possible impacts from hot summers, like the 2017/2018 New Zealand marine heatwave (Brandolino 2018, Thomsen et al. 2019a, Salinger et al. 2020).

4.1. Latitudinal distribution of foundation species

The effects of latitude affected dead shell and *Zostera* more than seaweeds. *Zostera* varied most across the latitudinal gradient (southern > central> northern, see Fig. 4.7.1 and table 4.8.1 for latitudinal and seasonal results and comparison to previous work see (Foster 2019, Siciliano et al. 2019)). At the landscape scale, 67% of photos had co-occurring seagrass and seaweed highlighting that these types of primary producers are ubiquitous in estuaries (Boström et al. 2006, Lyons et al. 2014). The pattern of dead shells (northern > central >southern) was opposite to the pattern for *Zostera*, and also found in Foster (2019). However, this study did not find differences in *Ulva* cover across latitudes, whereas Foster (2019) found seaweeds being most common in southern estuaries. These results are also contrasting several other studies that have shown higher seaweed abundances at higher latitudes (Santelices 1980, Santelices and Marquet 1998, Kerswell 2006, Keith et al. 2014, Guillemin et al. 2016, Foster 2019). The results for *Zostera* was consistent with previous work (Inglis 2003, Turner and Schwarz 2006). The finding that *Zostera* have higher cover in the southern estuaries may be because of different anthropogenic pressures (Turner 1996, Turner and Schwarz 2006, Turner et al. 2007), less thermal stress (Madeira et al. 2012, Thomson et al. 2015, Hughes et al. 2018, Oliver et al. 2018c, Kendrick et al. 2019) as high temperature can cause physiological stress to seagrasses (Eads et al. 2016, O'Mara and Wong 2016, Armstrong et al. 2020).

4.2. Latitudinal pattern in habitat-Interactions and invertebrates

I found that abundances, richness, and multivariate community structure of habitat-interactions was affected by stress, elevation level and latitude, where most habitat-interactions occurred at low elevations (Fig. 4.7.2). This pattern may occur because the foundation species often are more abundant and larger at lower elevation (thereby providing more habitat, see also Fig. 3.5.1) and because abiotic stress are reduced at lower elevations for most estuarine animals (Grant and McDonald 1979, Mitchell 1980, Shumway and Marsden 1982, Omori et al. 1998, Bertness et al. 2001, Jones et al. 2005, Marsden and Knox 2008). Importantly, molluscs like *Micrelenchus, Notoacmea, Diloma, Austrovenus,* and dead shells accounted for much of the data-variability highlighting the importance shell-producing animals in estuarine systems (Gutiérrez et al. 2003, Foster 2019). Deposition of dead shells on sediment surface provided habitat across spatiotemporal scales as found in a few other studies (Grange 1979, Gagné et al. 2008, Summerhayes et al. 2009, Ellis et al. 2017, Foster 2019), where shells can ameliorate desiccation stress and provide refugia from predators (Thomsen et al. 2016, Foster 2019). Overall, I quantified 575 interactions in the latitudinal survey (23% in northern estuaries, 45% in central estuaries and 32% in southern estuaries) where 25% were accounted for by *Micrelenchus tenebrosus* and 21% by *Notoacmea helmsi* alone. Little research have been done on these two taxa (Jones et al. 2005) but my results matches findings by Foster (2019), highlighting that these taxa should be studied more to better understand the ecology of estuaries on the South Island.

The habitat-interaction results were supported by results from sediment cores that showed that *M. tenebrosus* was found in high densities in seaweed and seagrass habitats, likely because these primary producers provide food for grazing, relief from predators, and at high tidal elevations also lower desiccation stress (Norkko 1998, Norkko et al. 2000, Cardoso et al. 2004, Thomsen et al. 2010a). My results also support a growing number of studies that have shown higher invertebrate abundances when seaweed and seagrass co-occur, probably because the two primary producers provide supplementary resources (Hooks et al. 1976, Gore et al. 1981, Pihl and Rosenberg 1982, Schneider and Mann 1991, Holmquist 1997, Thomsen et al. 2012b, Thomsen et al. 2013). Previous work (Siciliano 2018) that sampled the same sites in the same estuaries found relatively similar results, with more invertebrates in seaweed and seagrass habitats. However, Siciliano (2018) found higher biodiversity in northern estuaries, contrasting my results that showed higher biodiversity in southern and central low elevation sites, perhaps because I sampled in winter but Siciliano sampled in spring and fall.

Seagrass and seaweed habitats had strong positive effect on biodiversity, but on longer time scales seagrass provide a more stable habitat, because it has perennial roots and rhizomes and year-round production blades provide a more stable cover (Inglis 2003, Turner and Schwarz 2006, Foster), and therefore more stable habitat ameliorations (Grant and McDonald 1979, Omori et al. 1998, Bertness et al. 2001, Turner and Schwarz 2006, Turner 2007, Berthelsen et al. 2018). I noted that seagrass patches often were sparser with shorter leaves in the intertidal zone suggesting that the habitat-amelioration effect may be weaker here (Turner 1996, van Houte-Howes et al. 2004, Turner and Schwarz 2006). Out of 3933 counted invertebrates in the latitudinal cores, the two most common taxa - *Austrovenus stutchburyi* and *M. tenebrosus* were found in 24 and 23% respectively – once again highlight the importance of shell-forming species in estuaries (Johnson 1957, Trewin and Welsh 1976, Bailey et al. 1994, Gutiérrez et al. 2003, Summerhayes et al. 2009, Thomsen et al. 2016, Foster 2019, Beal et al. 2020).

4.3. Seasonal distribution of foundation species

There was relatively large variation in cover of *Zostera* and *Ulva* across seasons, but little variation in cover of dead shells. More specifically, both the landscape and close-up surveys found that *Zostera* where more abundant in winter but seaweed more abundant in summer as seen in other seasonal studies from this region (Siciliano 2018, Foster 2019). Temperature affects seagrass biogeochemical processes, reproductive strategies, dispersal pattern and overall health and is – with changing light conditions – the factor that drive seasonal changes in temperate seagrass beds (Bulthuis 1987, Johnson et al. 2003, Boström et al. 2006, Lee et al. 2007, Collier and Waycott 2014, Arias-Ortiz et al. 2018, Strydom et al. 2020). For example, Thom et al. (2014) found that temperature was the main drivers of variation in cover of *Zostera marina* in the Pacific Northwest and that temperature effects can be exacerbated during El Niño years (Thom et al. 2003, Thom et al. 2014). Furthermore, Moore et al. (2012) found negative synergistic impact on abundance of *Zostera* associated with small temperature increases and low light availability in the Chesapeake Bay, where deeper beds located close to the open ocean were least affected (Moore et al. 2012, Moore et al. 2014). Therefore, even small temperature increases (e.g., coupled with southern oscillation events and anthropogenic stress) could explain pattens shown in this study.

By contrast, *Ulva* was most abundant in summer months. Similar seasonal effects occur for many other estuarine seaweeds, typically attributed to a combination of high temperature,

high light and high nutrient levels that stimulate rapid growth and bloom formations (Raffaelli et al. 1998, Thomsen and McGlathery 2007, Marsden and Knox 2008, Abreu et al. 2011, Zhang et al. 2016). More specifically, similar patterns have been found in several other studies from the same area (Murphy 2006, Alexander et al. 2008, Foster 2019), documenting that *Ulva* cover consistently is higher in spring and summer. Importantly, *Ulva* recruits were often observed attached to cockle shells, suggesting that bivalves facilitate seaweed by providing attachment space for early life-stages (Callow et al. 2000, Genzer and Efimenko 2006, Alexander et al. 2008).

4.4. Seasonal pattern in habitat-Interactions and invertebrates

Overall, this study quantified 25,288 habitat-interactions across seasons in the two estuaries. There was a strong difference between the two estuaries with *Micrelenchus tenebrosus* and *Diloma subrostrata*. accounting for more than a quarter of all interactions and being abundant in the Avon Heathcote Estuary (Chapter 3, Fig. 3.5.3.5, Fig. 3.5.4.2). *D. subrostrata* and *M. tenebrosus* are endemic trochid gastropods that are common across elevational levels because they can tolerate high desiccation and thermal stress (Logan 1976, Mitchell 1980, Miller and Poulin 2001). These gastropods feed on macroalgae and benthic diatoms, where the former is more common on organic rich sediments and the latter more common in seagrass beds (Logan 1976, Powell 1979, Mitchell 1980, Hayward et al. 1999, Miller and Poulin 2001, Engels 2011). *M. tenebrosus* can also, as found here, be highly abundant on *Ulva* fronds (Murphy 2006, Thomsen et al. 2016, Siciliano 2018, Foster 2019). Differences in abundance of the two species across season could arise from differences in life history characteristics and recruitment (Rainer 1981, Holland et al. 1987, Platell and Potter 1996, Foster 2019). *D. subrostrata* and *M. tenebrosus* can also be biogenic habitat-formers themselves for cryptic taxa like bryozoan and small red alga (Thomsen et al. 2016, Foster 2019), and supporting studies from around the world that also has found that snails often facilitate other estuarine species (Schmitt et al. 1983, Voight and Walker 1995, Wahl 1996, Creed 2000, Chan and Chan 2005, Thieltges and Buschbaum 2007, Thomsen et al. 2010b, Wernberg et al. 2010b, Thyrring et al. 2013, Thyrring et al. 2015, Thomsen et al. 2016, Foster 2019). Thus, *D. subrostrata* and *M. tenebrosus* can function as mobile refugia for small invertebrates and seaweed and reduce desiccation stress in the upper intertidal zone (Thomsen et al. 2007, Wernberg et al. 2010b, Thyrring et al. 2013, Foster 2019).

Seagrass and seaweed supported higher abundances and diversity of invertebrates compared to mud cores as shown in many other studies (Boström and Bonsdorff 2000, Cummins et al. 2004, Boström et al. 2006, Thomsen 2010, Thomsen et al. 2012a, Lyons et al. 2014, Siciliano 2018). I also found greater richness and abundance at lower tidal elevations where abiotic stress is lower (Grant and McDonald 1979, Mitchell 1980, Lowell 1984, Boström et al. 2006, Bible and Sanford 2016). Richness (but not abundances) of invertebrates in cores was also higher when seaweed and seagrass co-occurred – a result that support many facilitation cascade studies that have shown positive impacts on biodiversity when foundation species cooccur (Altieri et al. 2007, Thomsen 2010, Angelini et al. 2011, Bishop et al. 2012, Dijkstra et al. 2012, Bishop et al. 2013, Angelini et al. 2015, Siciliano 2018, Thomsen et al. 2018b, Gribben et al. 2019, Crotty and Angelini 2020, Ravaglioli et al. 2021). Seasonal changes to seagrass density and leaf sizes can also affect invertebrate biodiversity (Laugier et al. 1999, Meling-López and Ibarra-Obando 1999, Guidetti et al. 2002, Lee et al. 2007, Siciliano et al. 2019), although invertebrates can adjust to such changes in habitat structure (Webster et al. 1998, Frost et al. 1999, Boström and Bonsdorff 2000). Battley et al. (2011) found that dense *Zostera muelleri beds on the Farewell Spit New Zealand, was inhabited by 37 taxa, whereas only three taxa were found in adjacent sand and very sparse seagrass beds. Although I found positive effects of Ulva on invertebrate biodiversity, the same seaweed can, when occurring in in thick mats, negatively affect invertebrates through hypoxia and smothering* (Norkko 1998, Raffaelli et al. 1998, Marsden and Bressington 2009, Vaquer-Sunyer and Duarte 2011, Lyons et al. 2014). *Overall, the abundance of invertebrates associated with foundation species where higher in winter than summer, contrasting several seasonal seagrass-invertebrate studies* (Heck 1977, Włodarska-Kowalczuk et al. 2014) *that have suggested that more abundant and larger seagrass over summer facilitate more invertebrates*. However, in New Zealand *Zostera* are often less abundant in summer and thereby provide less habitat (Turner and Schwarz 2006, Turner 2007). Furthermore, very hot summer can have negative impact on invertebrates and can therefore partly explain why I found more invertebrates in the winter cores (Allison 2004, Hopkin et al. 2006, Donner 2011, Sorte et al. 2011, Sunday et al. 2011, Madeira et al. 2012, Fraser et al. 2014, Smale et al. 2015, Thomson et al. 2015, Brandolino 2018, Chandrapavan et al. 2019, Fedaeff 2019, Kendrick et al. 2019, Miranda et al. 2019, Kim et al. 2020, Strydom et al. 2020).

4.5. General results

A key result from this study was that surface deposited dead shells were relatively common in all estuaries (Chapter 2) and that they modified and controlled many habitat-interactions (Chapter 3). For example, dead shell accounted for the highest abundance of interactions of any cover type across seasons. Dead shells can provide refugium for habitat-users from predators and abiotic stressors (Kidwell and Jablonski 1983, Kidwell 2002, Casebolt and Kowalewski 2018, Foster 2019). Most research on estuarine foundation species in New Zealand has focused on seagrasses (Turner and Schwarz 2006, Turner 2007, Jones et al. 2008, Nelson et al. 2015, Lohrer et al. 2016, Thomsen et al. 2016, Plew et al. 2020). However, understanding how estuarine communities are impacted by dead shell deposits should be explored in future studies. Another important result from the study was the regional differences observed between core samples. This contrast results from the North Island (de Juan and Hewitt (2011)). This study did not find regional differences in benthic communities, but that small scale habitat fragmentation had stronger effects. However, this study only sampled a smaller region. Differences between regions (Hanski 1982, de Juan and Hewitt 2011, Smale et al. 2017, Qin et al. 2020) and estuary types (Hume et al. 2007, Hume et al. 2016) characterized by different environmental factors (Berthelsen et al. 2020, Plew et al. 2020) highlight why baseline studies done across spatiotemporal scales are important. It is an important goal to understand how climate changes, heatwaves, eutrophication, and other anthropogenic stressor, affect estuaries, and standardized data collections across scales can help to achieve this goal (Caughlan and Oakley 2001, Nichols and Williams 2006, Berthelsen et al. 2018, Berthelsen et al. 2020).

4.6. Conclusion

Ulva and *Zostera* and highest cover in the southern region, dead shells in the northern estuaries, *Ulva* had highest cover in summer and *Zostera* and dead shells in winter. These three types of foundation species provided important habitat for invertebrates across latitudes, estuaries, seasons, elevation levels and sites. Interactions observed between these foundation species and habitat-users were generally lower compared to similar sampling done a few years before the hot summers of 2017/18 and 2018/19. Finally, I conclude that dead shells, a type of habitat that is poorly studied, are common across estuaries and that these shell deposits provide important habitat for many other species.

4.7. Figures

Figure 4.7.1. Foundation species change across latitudes.

The map shows general patterns in abundances of dead shells, the seaweed *Ulva* spp., and the seagrass *Zostera muelleri*, across latitudes (North, Central, South) and elevation levels (high and low) (see chapter 2 for details).

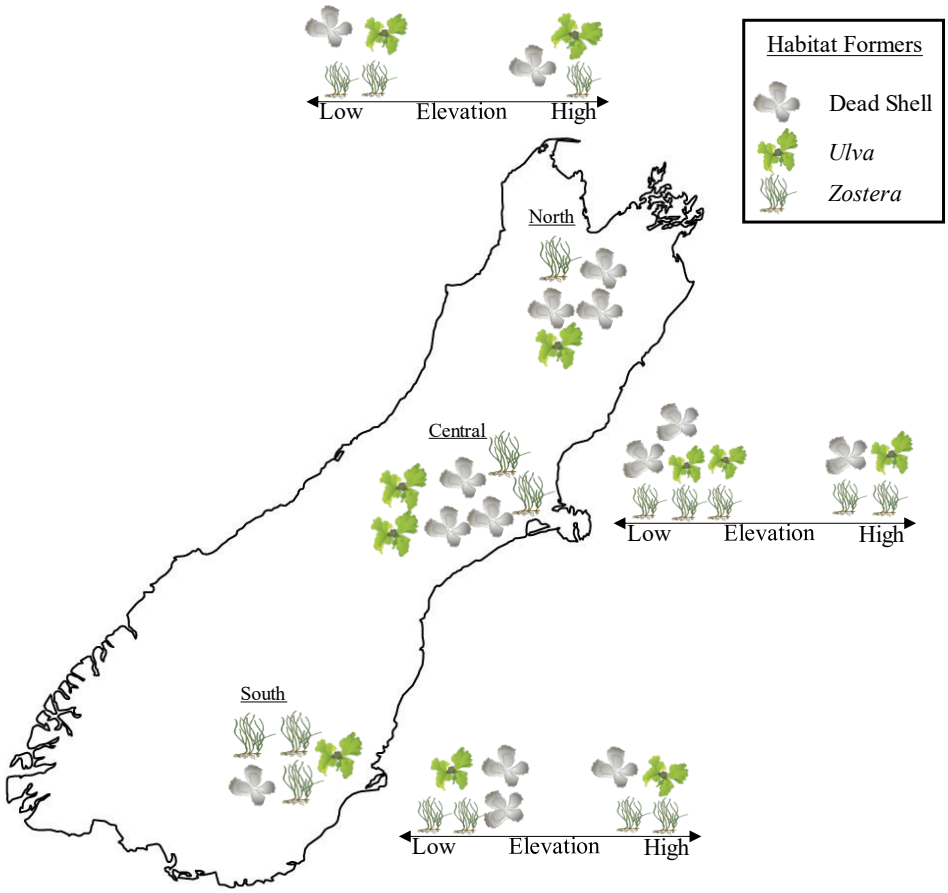
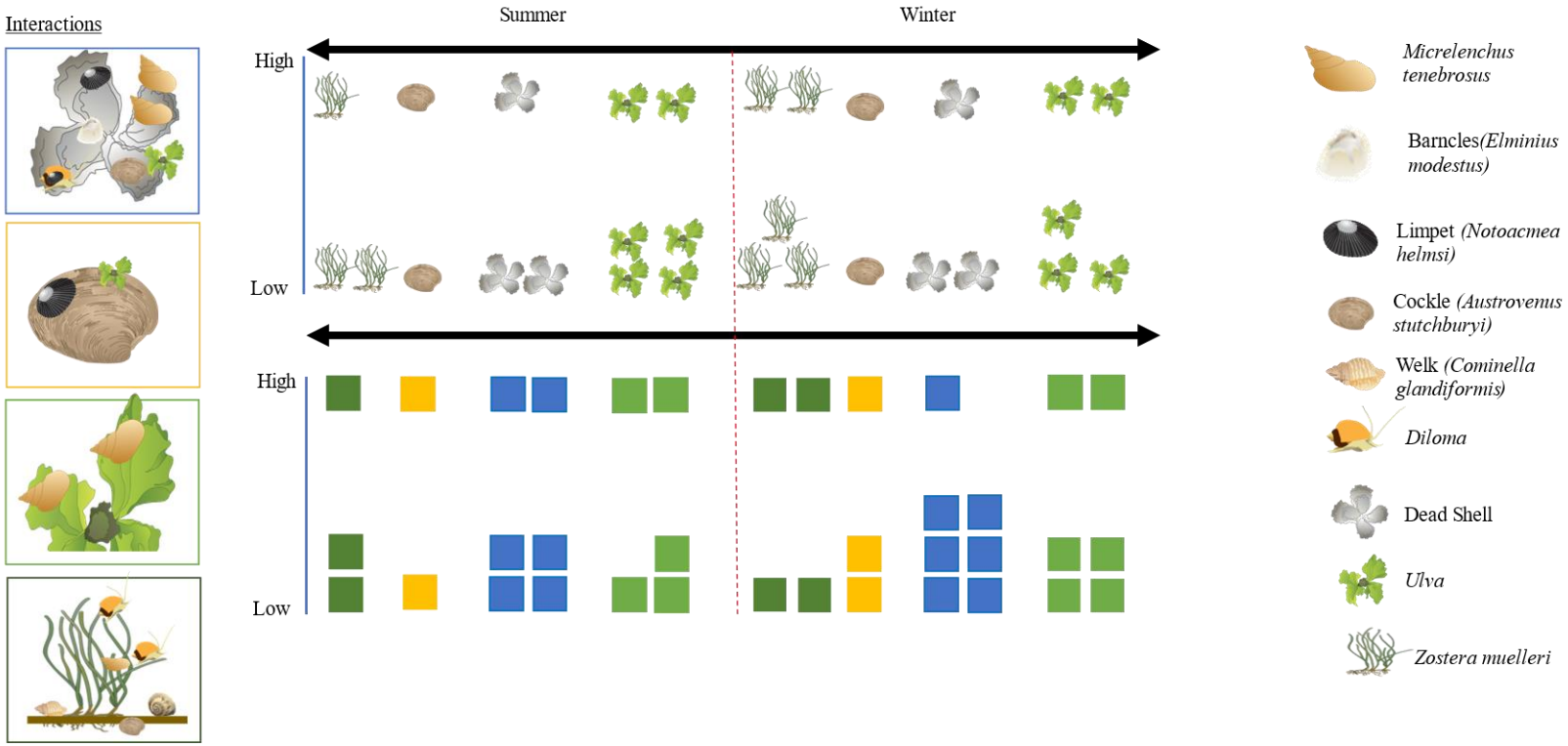


Figure 4.7.2. Habitat former and habitat-user interaction seasonal change.
Summary diagram highlighting changes to foundation species and habitat-interactions across seasons (left to write) and elevation levels (top to bottom). The top row reflects the relative abundance of the foundation and the bottom row (squares) the interactions between foundation species and habitat-users. Colour of the squares = most common interactions involving dead shell (blue), *Austrovenus stutchburyi* (yellow), *Ulva* (light green) and Zostera (dark green). High to low tidal elevation is indicated by the blue line and the separate summer and winter seasons (see Chapter 3 for details).



4.8. Tables

Table 4.8.1. Comparing key results from surveys done before and after the 2017/2018 hottest summer on record.

Comparing results from surveys done before (Siciliano 2018; Foster 2019) and after (this study) the 2017/2018 hot summer.

Bold rows highlight when results were similar between the different surveys. FS = foundation species, Inv. = Invertebrates. Core Abundance/Richness = invertebrates in core samples. Cover Type represents quadrat percent cover of *Zostera*, dead shells, or *Ulva*, or *Zostera* and *Ulva* cooccurring.

Survey Type	*Test Type*	*Cover Type/Core Type*	*Post-Heatwave*	*Pre-Heatwave*	*Study*
Latitudinal	**Quadrat FS Cover**	***Zostera***	**South > Central > North**	**South > Central > North**	**Foster (2019)**
Latitudinal	**Quadrat FS Cover**	**Dead shell**	**North > Central > South**	**North > Central > South**	**Foster (2019)**
Latitudinal	Quadrat FS Cover	*Ulva*	South = North = Central	South > North > Central	Foster (2019)
Latitudinal	Core Inv. Abundance	Bare	South > North > Central	North > Central > South	Siciliano (2018)
Latitudinal	Core Inv. Richness	Bare	Central > North >South	North > Central > South	Siciliano (2018)
Latitudinal	**Core** Inv. **Abundance**	***Zostera***	**South > Central > North**	**South > Central > North**	**Siciliano (2018)**
Latitudinal	Core Inv. Richness	*Zostera*	North > South > Central	North > Central > South	Siciliano (2018)
Latitudinal	Core Inv. Abundance	*Ulva*	South > Central > North	Central > South > North	Siciliano (2018)
Latitudinal	Core Inv. Richness	*Ulva*	Central > South > North	North > Central > South	Siciliano (2018)
Latitudinal	**Core** Inv. **Abundance**	***Zostera + Ulva***	**Central > South > North**	**Central > South > North**	**Siciliano (2018)**
Latitudinal	Core Inv. Richness	*Zostera + Ulva*	South > North > Central	North > Central > South	Siciliano (2018)
Seasonal	**Quadrat FS Cover**	***Zostera***	**Winter > Summer**	**Winter > Summer**	**Foster (2019)**
Seasonal	**Quadrat FS Cover**	**Dead shell**	**Summer > Winter**	**Summer > Winter**	**Foster (2019)**
Seasonal	**Quadrat FS Cover**	***Ulva***	**Summer > Winter**	**Summer > Winter**	**Foster (2019)**
Seasonal	Core Inv. Abundance	Bare	Winter > Summer	Summer > Winter	Siciliano (2018)
Seasonal	Core Inv. Richness	Bare	Winter > Summer	Summer > Winter	Siciliano (2018)
Seasonal	Core Inv. Abundance	*Zostera*	Summer > Winter	Winter > Summer	Siciliano (2018)
Seasonal	Core Inv. Richness	*Zostera*	Winter > Summer	Summer > Winter	Siciliano (2018)
Seasonal	Core Inv. Abundance	*Ulva*	Winter > Summer	Summer = Winter	Siciliano (2018)
Seasonal	Core Inv. Richness	*Ulva*	Winter > Summer	Summer = Winter	Siciliano (2018)
Seasonal	**Core** Inv. **Abundance**	***Zostera + Ulva***	**Summer > Winter**	**Summer = Winter**	**Siciliano (2018)**
Seasonal	**Core** Inv. **Richness**	***Zostera + Ulva***	**Winter > Summer**	**Winter > Summer**	**Siciliano (2018)**

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